THE HOPE REPORTS

VOL. XII

1911—1922

EVOLUTION, INSECT BIONOMICS (MIMICRY, VISION, EPIGAMICS, &c.) AND GEOGRAPHICAL DISTRIBUTION.

EDITED BY

EDWARD B. POULTON, M.A., D.Sc., Oxon, Sydney.

HON. LL.D. PRINCETON, HON. D.SC. DUNELM., F.R.S., ETC.

HOPE PROFESSOR OF ZOOLOGY IN THE UNIVERSITY OF OXFORD
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HONORARY MEMBER OF THE ACADEMY OF SCIENCE, NEW YORK
CORRESPONDING MEMBER OF THE SOCIETY OF NATURAL HISTORY, BOSTON, AND
THE AMERICAN ENTOMOLOGICAL SOCIETY

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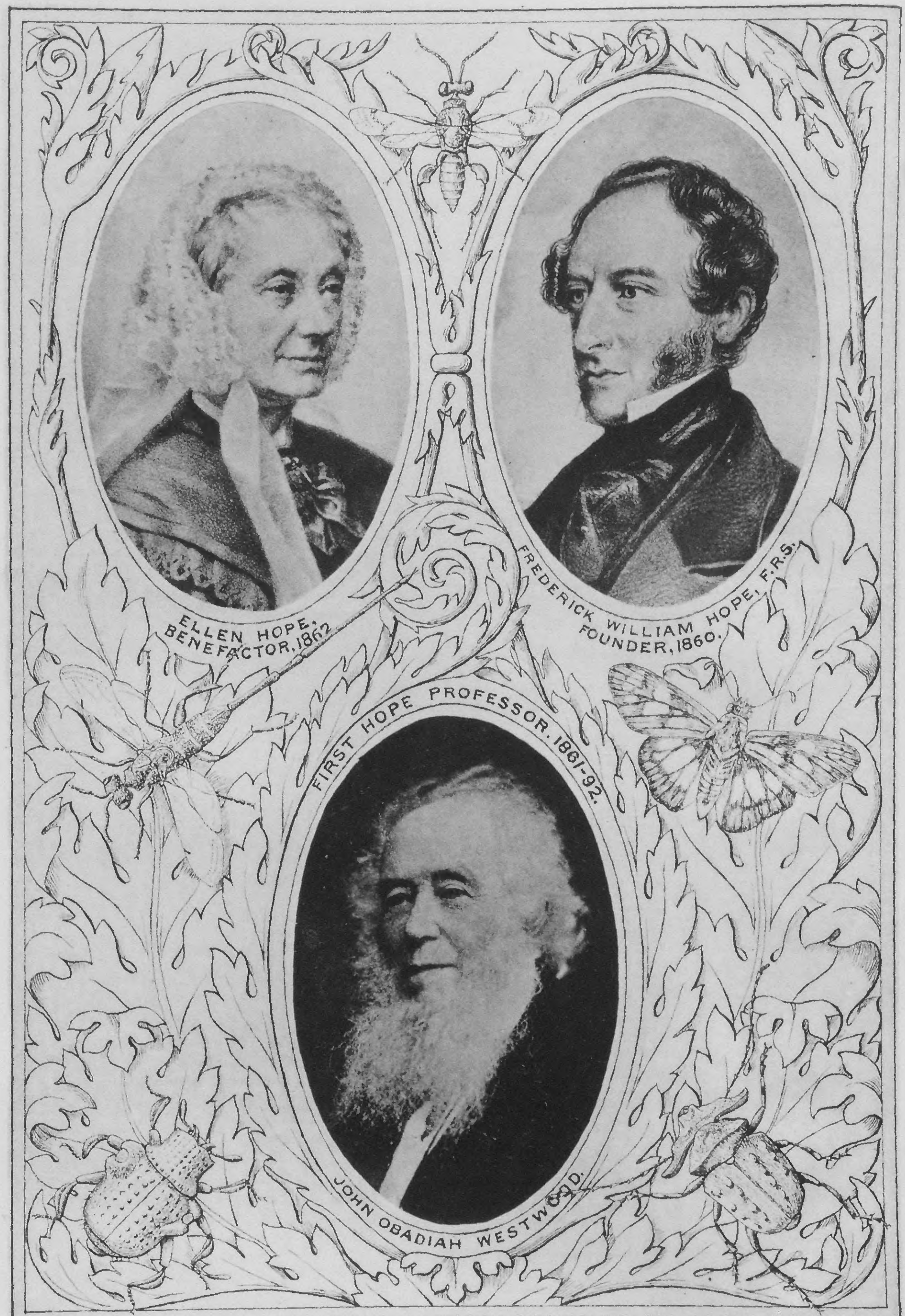
ELLEN HOPE,
BENEFACTOR, 1862
FREDERICK WILLIAM HOPE, F.R.S.
FOUNDER, 1860.
FIRST HOPE PROFESSOR, 1861-92.
JOHN OBADIAH WESTWOOD.
ALFD. ROBINSON, DEL.

THE MAKERS OF THE HOPE DEPARTMENT
OXFORD UNIVERSITY MUSEUM

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PREFACE.

THE first papers in this book, Nos. 2 and 3, give some account of the lives of two generous helpers of the Hope Department—Dr. G. B. Longstaff and G. A. James Rothney. They are included in Volume XII because it is devoted to the problems of Evolution and Natural History, and both were keen naturalists, delighting in observation and memory of the living world.

Nos. 4 and 5, by the Professor, deal with an American work on Evolution, proved after prolonged investigation to be an ingenious and elaborate forgery.

The succeeding sixteen papers—6 to 21—are concerned with various aspects of Mimicry in insects and especially butterflies.

Nos. 6 to 13, by the Professor, deal for the most part with objections which have been raised against the interpretation of Mimicry by Natural Selection.

No. 14, by J. C. F. Fryer, M.A., F.E.S., describes interesting observations on the enemies of butterflies in Ceylon.

Nos. 15 to 18, by Dr. F. A. Dixey, M.A., D.M., F.R.S., are chiefly concerned with the geographical aspects of Mimicry.

In 19, Dr. H. Eltringham, M.A., D.Sc., describes the systematic and mimetic relationships of the species in the South American butterfly genus *Heliconius*, while in 20, W. J. Kaye, F.E.S., discusses some of the conclusions. No. 21, by Dr. Eltringham, contains a brief account of a remarkable Australian moth pupa, the anterior part of which resembles the head of a wasp-like insect.

Dr. Dixey, in 22, gives an account of Seasonal Dimorphism in butterflies; Dr. Eltringham, in 23, of the urticating properties of the Goldtail Moth, *Porthesia similis*, shewing how the female collects with its anal tuft the larval spicules stored in the cocoon.

No. 24 is the important and well-illustrated memoir on butterfly vision, by Dr. Eltringham.

The next four papers deal with epigamic functions and structures:—25 and 26, by Dr. Dixey and the late Dr. Longstaff, being on the scents of male butterflies; 27, by Dr. Eltringham, on the remarkable male scent-organs in *Hydroptila* (Trichoptera); 28, by A. H. Hamm, F.E.S., on the extraordinary courtship of certain Empid flies.

Nos. 29 and 30, by Mr Hamm, are also concerned with the natural history of Diptera.

The remaining papers, 31—36, deal with the geographical distribution of insects, Nos. 31 and 32 being Commander J. J. Walker's Presidential Addresses to the Entomological Society of London—for 1919, on "The Fringes of Butterfly Life," for 1920, on "Some Aspects of Insect Life in New Zealand." No. 33, on the gradual spread of the North American butterfly *Danaida plexippus* over many parts of the world, and 34, on the occasional occurrence of butterflies in Iceland, are also by Commander Walker, R.N., M.A., F.L.S., F.E.S. No. 35, by Dr. Dixey, records observations made on a voyage to Australia, Ceylon and the Malay Archipelago; and 36, by F. C. Woodforde, B.A., F.E.S., Exeter, deals with some of the butterflies and moths of Eastern France.

EDWARD B. POULTON.

Hope Department of Zoology,
University Museum, Oxford.
July 9, 1923.

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3. George Alexander James Rothney, F.E.S. Obituary by the Professor. (*Ibid.*, 3rd Ser., Vol. VIII., May 1922, p. 113.)

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7. Mimicry and the Inheritance of Small Variations, by the Professor. (From "Bedrock," Vol. II., No. 3, October 1913, p. 295.)

8. Experimental Evidence for the Hereditary Transmission of Small Variations such as would be required to initiate a Mimetic Resemblance in Butterflies, by the Professor. (From "Report, British Association," Hull, 1922, p. 372.)

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15. The Geographical Factor in Mimicry, the Presidential Address to the Zoological Section of the British Association, with Plate III., by Dr. F. A. Dixey, M.A., D.M., F.R.S. (From "Report, British Association," Bournemouth, 1919, p. 199.)

16. The Geographical Relations of Mimicry, by Dr. F. A. Dixey. (From "Report, British Association," Birmingham, 1913, p. 518.)

17. On Mimicry in Certain Butterflies of New Guinea, by Dr. F. A. Dixey. (From "Transactions of the Entomological Society of London," 1918, p. 118.)

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19. On Specific and Mimetic Relationships in the Genus Heliconius, L., with Plates XI.—XVII., by Dr. H. Eltringham, M.A., D.Sc., New College, Oxford. (*Ibid.*, 1916, p. 101.)

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22. Seasonal Dimorphism, by Dr. F. A. Dixey. (From "Proceedings of the South London Entomological and Natural History Society," 1916–17, p. 1.)

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25. ~~The Scents of Butterflies, a Friday Evening Discourse, Royal Institution, March 3, 1911, by Dr. F. A. Dixey. (From "Proceedings of the Royal Institution," 1911, p. 73.)~~

26. Further Notes on Scents in Butterflies, by Dr. G. B. Longstaff, M.A., D.M., F.R.C.P. (From the "Entomologist's Monthly Magazine," 2nd Ser., Vol. XXV., January 1914, p. 1.)

27. On the Histology of the Scent-Organs in the Genus Hydroptila, with Plate XXII. (two copies on different paper*), by Dr. H. Eltringham. (From "Transactions of the Entomological Society of London," 1919, p. 420.)

28. A. H. Hamm's Observations on Empidae and their Prey in Relation to Courtship, by the Professor. (From "Entomologist's Monthly Magazine," 2nd Ser., Vol. XXIV., August 1913, p. 177.)

29. A Ribbon-making Fly: the Oviposition of Ceratopogon nitidus, Macq., by A. H. Hamm, F.E.S. (*Ibid.*, 3rd Ser., Vol. V., March 1919, p. 66.)

30. Observations on the Horse Bot-fly, Gastrophilus equi, F., by A. H. Hamm. (*Ibid.*, 3rd Ser., Vol. V., October 1919, p. 229.)

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* One plate shows the details better than the other, but the latter is believed to be more lasting.

31. The Fringes of Butterfly Life, the Presidential Address read before the Entomological Society of London at the Annual Meeting, January 21, 1920, by Commander James J. Walker, M.A., R.N., F.L.S. (From "Proceedings of the Entomological Society of London," 1919, p. lxxxix.) The map which accompanied the original publication was unsatisfactory and is omitted.

32. Some aspects of Insect Life in New Zealand, the Presidential Address read before the Entomological Society of London at the Annual Meeting, January 19, 1921, by Commander J. J. Walker. (*Ibid.*, 1920, p. cvii.)

33. The Geographical Distribution of Danaida plexippus, L. (Danais archippus, F.), with Especial Reference to its Recent Migrations, with map, by Commander J. J. Walker. (From "Entomologist's Monthly Magazine," 2nd Ser., Vol. XXV., 1914, July, p. 181 ; August, p. 185 ; September, p. 224 ; October, p. 233.)

34. On the Occasional Occurrence of Butterflies in Iceland ; with Notes on the Lepidopterous Fauna of the North Atlantic Islands, by Commander J. J. Walker. (*Ibid.*, 3rd Ser., Vol. VIII., January 1922, p. 1.)

35. Notes of a Voyage to Australia, Ceylon, and the Malay Archipelago, July–November, 1914, by Dr. F. A. Dixey. (*Ibid.*, 3rd Ser., Vol. II., 1916 · January, p. 10 ; February, p. 46 ; March, p. 49 ; May, p. 119 ; June, p. 121.)

36. Some Lepidotera from Eastern France, by F. C. Woodforde, B.A., F.E.S., Exeter College, Oxford. (*Ibid.*, 3rd Ser., Vol. VII., March 1921, p. 51.)

[*Reprinted from the 'Entomologist's Monthly Magazine,'* 3rd ser., vol. vii.]

Obituary.

George Blundell Longstaff, M.A., M.D., F.L.S.—On May the 7th last, after a long illness, died at his residence, Highlands, Putney Heath, Dr. George Blundell Longstaff in his 73rd year. The funeral, attended by a large gathering of relations, friends, Fellows of the Entomological Society of

London, and others who had been associated with him from time to time in work of various kinds, took place on the following Thursday at Putney Vale Cemetery.

So passes the oldest and one of the dearest of my friends; and from among contemporary British entomologists surely one of the most enthusiastic, generous, and personally attractive votaries of the science that engages our study. What Longstaff did for Entomology—more specially what he did for the work and collections in the Hope Department of the Oxford Museum—I will leave Professor Poulton to say. On such points he will speak with authority. In this memorial note which the Editor has so kindly asked me to contribute, I confine myself to a slight appreciation of the character of my friend as it impressed itself upon me with increasing force through a close unbroken intimacy of over fifty years.

It was in the October term of 1868 that he and I first met as Freshmen at New College, Oxford. Two main interests brought us into companionship—a love of Art, and a love of Natural History. Longstaff had come up from Rugby, having gained at New College an open Natural Science scholarship. During his school years he had devoted much serious care to observing insect life alike in the neighbourhood of Rugby and his home at Wandsworth. And here it is interesting to note how thus early it was the difficult group of the *Tortricina* which peculiarly attracted him; so that, indeed, he became filled with an ambition of some day specializing upon it, and producing a standard work dealing exhaustively with the group. Alas! *dis aliter visum.* He had not been long an undergraduate before a shocking accident deprived him of the sight of one of his eyes, and put a stop for ever to all such schemes of scientific study as would involve close microscopic investigation. Well, the way in which he bore this bitter stroke of fate was characteristic of him. Far from sitting down a disheartened rebel, he at once pulled his energies together, and addressed himself cheerfully to other lines of study and work for which minute eyesight was not indispensable.

Certainly this indomitable cheerfulness or buoyancy of temperament, united as it was with an unusual power of perseverance, and what one may without exaggeration call a passion for thoroughness, went far towards keeping George Longstaff throughout his life not only the busiest of men, but the most enthusiastic and youthful. No one came across him even to the last but was struck by his alert vivacity, both physical and mental. It was hard to associate him with the thought of age. Let me here illustrate this by reference to a little incident. When the London County Council was first established, Longstaff was elected one of its members; and, when later on the difficult business of bringing in the New Building Act occupied its attention, he was appointed chairman of that important committee. I remember one day asking a builder on the Council whether he chanced to know my friend. "Know him!" he replied, "I should think I did. Why, somehow or another, Dr. Longstaff has learned to understand pretty well as much about the practical side of the building trade as we builders ourselves do!" Of course he had. For indeed George Longstaff was a man who never did anything by halves. Whatever he took in hand, he would first of all set himself to find out all he could about the nature and right conduct of it, and then go on seriously to see the thing through. This surprising thoroughness was assuredly a leading note in his character. But to those who had to work with, or for, or under him, it led to no hectoring dominance of behaviour. It was balanced by an equally surprising kindliness of heart, by a sympathetic understanding and consideration of other people's ideas, and by a true man's regard for their knowledge, individual point of view, and sincerity of effort.

Supposing that eye-accident at the outset of his career had never happened. Well, I have sometimes asked myself—what then would my friend have done and become? Possibly he would have devoted himself to science exclusively. Nay, I fancy indeed this more or less was his ambition. And with his intellectual alertness, his patience and accuracy in observation, his determined thoroughness, supplemented, as these would have been, by means at hand enabling him to prosecute his investigations unrestrictedly—there is no doubt he would have gone far, establishing himself as an enviable authority in this or that chosen specialized department. Yet, after all, would he have thus served his nation better than he actually did serve it? May it not be that the very restrictions and diversity of interests this apparently most lamentable misfortune imposed on him, only rendered his life's service the more valuable by compelling it to be more varied and diffusive?—SELWYN IMAGE: *May 22nd*, 1921.

The late G. B. Longstaff.—There is little for me to add to the excellent and appreciative notices of my friends, Professors Poulton and Selwyn Image. My relations with George Longstaff began in the year 1878, when I joined him in some work on the germicidal properties of certain advertised disinfectants, and afterwards collaborated with him in many investigations in the Registrar-General's Department of Somerset House, which afterwards bore fruit in his published volume of "Studies in Statistics." It was not long before we discovered each other's interest in entomology, and from that time we became constantly associated in the pursuit of that branch of natural history. I was with Longstaff when he acquired the beautiful estate in North Devon where much of his life was passed, and I well remember the keenness with which he threw himself into the study of the Lepidopterous fauna of the district. His published list of the Mortehoe *Lepidoptera* embodies the result of many years' assiduous collecting and observation, conducted under the serious difficulty of impaired eyesight. He was an admirable field naturalist—patient, active, and enterprising. He had a sovereign contempt for what he called "feather-bed sugaring," and some of our nocturnal expeditions among the North Devon cliffs were not unattended with danger to those less sure-footed than himself. His "Butterfly-hunting in Many Lands" contains ample evidence of his interest in the scientific bearing of the facts which he amassed with so much energy and insight. Of his quality as a student of tropical fauna I had good reason to judge in the course of the travels that we undertook together in South Africa, a record of which forms part of the work last mentioned. It was characteristic of him that so soon as any point of biological importance was brought to his notice, he at once began to consider how far it might be illuminated from entomological data, and to devise plans for acquiring and making available the necessary evidence. In carrying out these plans he found scope for the operations of an unusually active mind and a thoughtfully generous disposition. "Large was his bounty, and his soul sincere."

A man of such wide interests and so sympathetic a nature was bound to make hosts of attached friends, by whom his death is felt as a grievous personal loss. "*Exstinctus amabitur idem.*"—F. A. D.

Although Dr. G. B. Longstaff's name was well known to me as that of an Oxford man distinguished for his public service, an authority on statistics, and a generous benefactor inspired by far-reaching sympathies, our friendship only began in 1904, after his return from his travels in the East. From that time we met continually, both in Oxford and London, and he was always planning to help the Hope Department in many ways. He realised at once, what is often forgotten by those who give to museums, that the captures he was sending in thousands meant labour and time, and that the Department, like most, I might say all, museums, was understaffed. So, after giving immediate help to meet the extra strain, he made it possible in ~~1895~~ for the Department 190
to employ an additional assistant, contributing the salary each year until 1909, when, by an endowment of £2400, he assured its permanence. The trust deed is a model one in its simplicity and in the care to ensure that, whatever may happen in the future, the income of the fund will always be of the highest utility to the Hope Department. Then he would often buy books for the library and would send lists of works in his possession in order that the Department might select what it needed. In 1910 his help made it possible to acquire the fine collection of British *Rhynchota* made by the late Edward Saunders, F.R.S.

But George Longstaff did far more than this for the University Collections at Oxford. What I have spoken of above—as also his generous gift of £1000 to the Entomological Society shortly before his death—could have been done by any rich man, although too few in this country are inspired to use their wealth for such ends. Longstaff gave also the personal service of an able and intensely active mind. In planning his travels he would consider the needs of the collections. Then, before setting out on his second journey in 1905, he devised a special form of note-book, strongly bound with leather back and corners, ruled for date and locality and notes. Eleven of these exist in the Department, and, from their data, each specimen has been labelled with all essential facts, and also by a reference number can be compared with the original record. It it pathetic to look at the last entries, made with difficulty and failing sight, about a year before his death. Then, when he returned home he would work out his collections, continually visiting the British Museum for the purpose, and would come to Oxford for their incorporation. In 1907 and 1908, realizing how greatly we were handicapped by the want of an up-to-date catalogue of *Satyrinae* and *Hesperidae*, he set to work and made a complete list of all the species of both groups in the British Museum. His manuscript list of *Hesperidae* contains 2244 species. Indexed by the late Robert Shelford, and bound, it has been of the greatest value. It is in constant use.

Although our friendship sprang from scientific interests in common, one could not come into contact with George Longstaff without feeling the stimulus of an intensely active, energetic, sympathetic nature. There was his public spirit and energy during the war, his interest in the police and in institutions for the insane, his love of art and of his garden and the beautiful open space around it. I shall always think with pleasure of the last time I walked with him in his garden, in the summer of 1920, and of his delight in recognizing a "Large Skipper" behind the rockery.

His was, we may be sure, a very happy life, and many are happier because of it.—E. B. P.

It may be added that Dr. Longstaff's association with our Magazine commenced with the first volume, in which a brief note on *Lepidoptera* taken near Wandsworth appears on p. 76. Further articles by him are scattered through our earlier volumes, including very interesting papers on the *Lepidoptera* of Rannoch, in conjunction with the late J. B. Blackburn (vol. v, pp. 221–223), and of Forres (vol. vi, pp. 214–216). In more recent years his contributions to our pages include the narrative of his collecting experiences in Venezuela (vol. xliv, pp. 69-76, 118-123) and in the Egyptian Sudân (vol. xlvii, pp. 119–127, 194–202), which are embodied in his fine work "Butterfly Hunting in Many Lands"; and a valuable paper, supplementary to the section dealing with that interesting subject in the same book, "Further Notes on the Scents of Insects" (vol. l, pp. 1–8).

Dr. Longstaff was a Fellow of many learned associations, including the Linnean, Geological, and Entomological Societies; of the last-mentioned, which he joined in 1904, he was Vice-President in three separate years, 1909, 1915, and 1917.—Eds.

[*Reprinted from the 'Entomologist's Monthly Magazine,'* 3rd ser., vol. viii.]

George Alexander James Rothney, 1849–1922.—G. A. James Rothney, who died on January 31st in his 73rd year, was a keen entomologist, especially interested in the Aculeate Hymenoptera, and one whose broad outlook took in many sides of his favourite science—that of the naturalist perhaps even more than the keen collector and student of systematics; the artistic side, revealing the setting of the insect world in the whole scheme of nature; above all, the human and personal, delighting in memories of his scientific comrades.

Where shall we find so fine a picture of Edward Saunders as that given by him in the "Proceedings of the Royal Society" (B. vol. 91, p. xvi)?—"I can see him now as he was in 1868 to 1870, looking so very young and boyish, but standing up and reading learned papers at the Entomological Society on the *Buprestidae*, listened to and holding his own with the giants of those days." And then memories of his later years and home-life, and the conclusion:—"He was the kindest helper and friend that anyone could have." One thinks, too, of Rothney's pleasure in recovering and placing near his own in the Hope Museum at Oxford, a collection recalling, as he wrote, "a memory of good, cheery old Fredk. Smith, one of the dearest and most interesting of men."

The naturalist and artistic sides of his nature are evident in his graphic story of a tremendous flight of Winged Termites at Barrackpore—"a real 'Brock's benefit' in White Ants," and in the delightful "picture-memories" recorded in this Magazine (1920, p. 175), memories which, as he said, "I love to dwell upon now my collecting days are over."

Rothney's great collection of Oriental *Aculeata* was begun in 1872, the year when he sailed to the East in the service of C. W. Scott & Co., merchants, of Calcutta, soon to become John Dickinson & Co. His own captures were chiefly made in Barrackpore Park near his house, also in Calcutta, Mussoorie, Allahabad, and N. W. P. The collection is also rich in specimens from other famous entomologists—Bates, Bingham, Cameron, Forel, and F. Smith, and includes a very fine series taken by natives in the Khasia Hills, Assam, and extremely rich in types of new species not only among the *Aculeata* but also the *Phytophaga* and *Parasitica*. The ants, which are a special feature, include species from many other parts of the world. Together with this splendid collection in its cabinet he presented nearly 100 volumes and numbers of unbound separata, forming a library of the Oriental Hymenoptera, including all publications concerned with the Rothney collection, also 14 volumes of his own papers, correspondence, and notes, chiefly on Indian Hymenoptera and Lepidoptera. He also presented his own series of the Trans. Ent. Soc. Lond., dating from 1868, the year of his election, and arranged for its continuance and uniform binding until the end of 1922. "1868–1922 inclusive is a pretty good show" he wrote on December 31st. In addition to the Hymenoptera, he gave fine series of other Oriental insects and a small cabinet containing his British Aculeates, including the first male and female of *Formica exsecta* taken in Britain, and the example, for many years unique as a British insect, of *Odynerus herrichii* (=*basalis*) taken in Dorset in 1868.

I well remember the extraordinary care and interest he took in the transport by road of these collections to Oxford, personally superintending the packing in the van and arranging that it should arrive so that I could superintend the unpacking and at once send him a telegram when all was safe. I recall, too, the characteristic generosity with which he sent a present to the carter when the telegram came—generosity combined with wise foresight, for the man had been told what he might expect if he used all care and discretion. And he never lost sight of or forgot his collection, but would seize every chance of adding to it by the purchase of further series of Hymenoptera, especially pleased when they were Oriental species from new districts, or insects of all kinds from ex-enemy countries. These generous gifts were continued in the last years of his life and referred to in letters dictated a few weeks before his death. He bequeathed £150 to the Entomological Society, and £50 to the Hope Department to provide further accommodation for his favourite Oriental Hymenoptera.

He kept all his keen interest in natural history up to the end. A fortnight before his death he listened to a long scientific paper read to him by his daughter and only finished when it was nearly midnight, and dictated a letter telling of his interest in it, and his pleasure at his daughter's interest. And a few days earlier he had supplied further details concerning the capture of rare British insects, and made an important correction in the data previously given. "I don't know how it is," he wrote, "but as one gets older and towards the end of the lane one turns to one's first love—*British Butterflies.*"

It was the same with his other great interest—Rugby football. After hearing the summary of current events in the newspaper he would always say "Now turn to the football news." Rothney was one of those wise Englishmen who know well that the worst thing to do in the Tropics is to live a sedentary life chiefly occupied in cursing the weather. He was the first to start distance running in India; he introduced Rugby Football into Calcutta in the year of his arrival, and, when Captain and Secretary of the Club in 1878, it was at his suggestion that the Calcutta Cup was presented to the Rugby Union, to be competed for annually by England and Scotland.

With his brain clear and active as ever he died as he would have wished, very quietly; with his two daughters by his side.—E. B. P.

4

[*Extracted from the* PROCEEDINGS *of the* LINNEAN SOCIETY
OF LONDON, Session 1912-13.]

A REMARKABLE AMERICAN WORK UPON EVOLUTION AND THE GERM THEORY OF DISEASE.

THE PRESIDENTIAL ADDRESS
READ BEFORE THE
LINNEAN SOCIETY OF LONDON
AT THE
ANNIVERSARY MEETING,
MAY 24, 1913,

BY

PROFESSOR EDWARD B. POULTON.

LONDON:
PRINTED BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.
1913.

PRESIDENTIAL ADDRESS, 1913.

About two months ago when I was thinking over various possible subjects for this address, there arrived by post—just at the psychological moment—an American pamphlet, sent by my friend, our illustrious Fellow, Dr. Alfred Russel Wallace. Accompanying the pamphlet was the following very kind letter, referring to James Cowles Prichard's * anticipation of modern views on evolution.

Old Orchard,
Broadstone,
Dorset.
April 2, 1913.

My dear Poulton,

About two months ago an American sent me the enclosed booklet, which he had been told was very rare and contained an anticipation of Darwinism.

This it certainly does, but the writer was highly imaginative, and, like all the other anticipators of Darwin, did not perceive the whole scope of his idea.

His anticipation, however, of diverging lines of descent from a common ancestor and of the transmission of disease germs by means of insects, are perfectly clear and very striking.

As you yourself made known one of the anticipators of Darwin, whom he himself had overlooked, you are the right person to make this known in any way you think proper. As you have so recently been in America, you might perhaps ascertain from the Librarian of the Public Library in Boston or from some of your biological friends there what is known of the writer and of his subsequent history.

If the house at Down is ever dedicated to Darwin's memory, it would seem best to preserve this little book there; if not you can dispose of it as you think best.

With best wishes,
Yours very truly,
Alfred R. Wallace.

Referring to the last paragraph, Dr. Wallace now agrees with me that the library of the Linnean Society is the most appropriate place for the work.

The booklet had been sent, on Feb. 6, 1913, as a kind of 90th birthday present to Dr. Wallace, by Mr. B. R. Miller, an American gentleman who has always taken a lively interest in the subject of evolution. In a later letter, dated May 12, Mr. Miller writes to me:—"I remember the bookseller I bought it of saying that it

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* Poulton's Essays on Evolution, Oxford, 1898, p. 173. Prichard's anticipation was discovered by the late Dr. Maurice Davis, J.P.

was an old work and had been through many hands; this was in a Mr. W. Davie's book store in either Cleveland or Cincinnati,—one or the other Ohio town, in 1891 or 1892."

The pamphlet, which appeared to be very old, although in an excellent state of preservation, bore the following words on both cover and title-page.

SHALL WE HAVE COMMON SENSE

SOME

RECENT LECTURES

WRITTEN AND DELIVERED BY

GEO. W. SLEEPER.

BOSTON:

WM. BENSE, PRINTER.

1849.

The contents entirely bore out Dr. Wallace's words. Supposing the work to be genuine, I doubt whether so much of pregnant thought and penetrating imagination has ever before been recorded in so small a compass. The pamphlet measures 4 inches in width by just under $5\frac{1}{2}$ in height, the printed surface of 32 out of the 36 pages measures $2\frac{5}{8}$ inches by $4\frac{3}{8}$.

The remaining 4, being first and last pages, hold fewer lines of print. The type is far from small and spaced so that a complete page holds 27 lines.

The pamphlet contains a brief introduction, not included in the 36 pages referred to above, and two lectures stated to have been delivered in Boston in 1847.—"The Origin of Life and the advance of civilization," and "The Dangers of the Unseen."

Within a space thus limited, the ideas in the following pages are propounded. The author's words, except in the concluding paragraph of the booklet, are quoted without comment, but I have printed in italics at the head of each section the various subjects with which he deals. I have also inserted a few words in square brackets and added one or two footnotes in order to show the relationship between some of the author's sentences or to make some brief explanation.

Lecture I.

THE ORIGIN OF LIFE

AND THE ADVANCE OF CIVILIZATION.

i. *The Origin of Life in minute particles scattered through space—a view similar to that brought forward by Arrhenius in 1906.*

". . . . . . Life owes its faint beginning to primal germs. These germs I hold to be infinitesimally minute living atoms pervading the entire terrestrial atmosphere; and, perhaps, the entity of the Cosmos.

"Perishable themselves, each is the common carrier of the principle of Life which is indestructible and eternal, ..." (p. 3.)

ii. *Natural Selection.*

"Arranging themselves in strict obedience to dominant Natural laws of which we have but little knowledge, in a vastness of Space of which we have no intelligent conception, and exhibiting an almost unmeasurable minuteness reducing our feeble powers of comprehension to appalled nothingness, these germs are slowly developed, altered and perfected during an immensity of periods of time compared to which the six thousand years of the Bible is but a trifling era—a pebble ou the sea shore; a tiny star in the Milky Way.

"These germs of life and the individuals growing out of them, were constantly experiencing change. Weakened by exposure and attack they were only preserved unmodified for a brief (though variable) period by means of the more or less effectual resistance they were able to offer to climatic conditions, changes of food, convulsions and transformations of Nature and the destructive inroads of overpoweringly hostile forms of reptile, piscine or animal Life. . . . . . ." (p. 4.)

"Primal matter to zoophyte, to crustacean, to fish, to saurian, to mammal and to Man! the inferior forms disappearing when their allotted work was done and the improved era no longer warranted their then inutile existence just as the platysoma of the Old Red Sandstone vanished in the Magnesian Limestone; or else becoming dwarfingly modified previous to extinction: similarly to the diminution of the seventy foot iguanodon into the four foot and perishing iguana which has outlived the age and environment which called its giant ancestor into being.

"In this ever recurring disappearance, or modification, of animal and vegetable forms there is nothing strange. Everywhere about us we see waged the pitiless battle for life of which it is the inevitable outcome. Just as the dandelion, the plantain and the burdock extend their broad leaves o'er the verdure of the meadow, starving and exhausting the grasses around them; . . . . . . so there is a contiuual process of elimination and substitution going on in the great laboratories of Nature; the useless perish, the useful live and improve, although our conception of what is useful and improving is often opposed to Nature's.

"All Geology indicates assured progress by its presentation of higher and higher generations of exalting forms, each remarkably suited to the peculiar age in which it appeared at its best . . . . . ." (pp. 8–10.)

iii. *Recapitulation.*

"The wonderful progressive presentation of forms ascending from day to day in the scale of organized beings exhibited by our species in the fœtal state and remarked by the physiologist, is another substantiation of my theory.

"Man, in the womb, passes through all the embryo forms of the types of the known divisions of animated Nature: first but a germ, he then resembles mollusk, fish, reptile, bird, rodent, ruminant, and batrich *, finally assuming unmistakeable features of the human animal. Thus we see a significant panorama of the momentous changes which occurred in the course of ages displayed in the short space of nine months in the mysterious womb." (p. 8.)

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* Evidently a printer's error for "batrach" and referring to a fanciful resemblance of the fœtal face to that of a frog.

iv. *The antiquity and origin of Man: his development, not from the Anthropoids directly, but, on diverging lines, from an ancient common ancestor.*

"...... And it is also fabled that all this work of Creation occurred but six thousand years ago! Which Creation, the state of civilization in India and China some five thousand years back, is sufficient to disprove without the abundant aid derived from Geological evidence; all proving an inconceivably ancient history for Man." (p. 2.)

"...... Man and the Ape are co-descended from some primary type, ..." (p. 6.)

Remembering "that it is not to the higher evolutions of Man nor to the lower * variations of the Monkey that we must look in this matter, but to just the reverse of each." The lecture continues "And then in many respects a striking parallel is observed to exist between the 'lord of creation' and his Quadrumana relatives the Chimpanzee and the Ourang Otang which clearly establishes the extremely rational view I have advanced and enables us to experience very little difficulty in tracing back these kindred creatures to a remote, an ancient, but a general stock; although exactly what that common forefather was is as likely to forever remain as profound a mystery as the astounding problem of how the beginning of things could take place or the absolute ending of all matter can ever occur!

"We have never found any living or fossil link to form a chain between Man and the Ape, nothing to close the gap separating the two related animals like Owen's rhynchosaurus bonds the avines to the saurians, and the pliosaurus unites the pterodactyle to the crocodile. I doubt that any such creature will be discovered; to my mind there never was occasion for its existence: more likely some relic of an, at present, unknown animal proving to be the forerunner of both species, will be exhumed out of the debris of an age immediately antecedent to both: ......" (pp. 6–8.)

"I feel assured that skeletons or rock-preserved hairy specimens of this ancestor of the two species will ultimately be excavated from the strata preceding that in which remains of Man and of the Monkey have been found, ... The greater perishability and much more restricted production and distribution of the human frame in those remote ages, together with the very limited extent of the exploration of this but recently thrown open field have so far precluded success." (p. 11.)

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* This and the preceding five words are so faintly printed as to be almost unrecognisable, but it is believed that the reading adopted above is correct. [Since confirmed by reference to a more clearly printed copy kindly lent by Mr. J. F. Sleeper.—E. B. P. Aug. 12, 1913.]

v. *The germinal origin of characters, and the persistence of germ-life.*

"But our parallel of comparison of Man with the Simians is effectually arrested by a threefold, irremoveable, barrier: the possession of progressive, deductive and inventive Reason; the acquirement of extensible and transmissible Speech; and the innate knowledge of the formation and use of Tools; attributes resident solely in the spermatozoa and ovum of the human species, and absolutely inseparable therefrom. So I am spared the unpleasantness of announcing anything so distasteful, to you, as that the monkey was parent or progeny of Man; thus, this Scylla and Charybdis being happily steered past, I merely find it necessary to reaffirm my fixed belief in the gradual origination of both from a general parent, each distinct from birth and each preserving that distinctiveness unto the present epoch, modified somewhat, it is true, in the instance of the human individual owing to his germ-endowment with the rudiments of primarily cultivatible and incalculably higher functions." (pp. 10–11.)

"Spiritualism plays no part in the great drama of this our life. Indeed, the sole phenomenon approaching to such is the departure of the life-germ from a perishing frame but to begin anew in another or an allied form. For nothing is lost in the vast economy of Nature: all things suffer but a transient change of form: thus the life germ resident in Man transmitted to his descendants, goes on existing indefinitely throughout all Time's infinitude of years; just as his Thoughts, those Genii children of his prolific brain, continue to live on ages and ages after that transitory organ has mouldered away into the dust of the long ago; and thus, and only thus, is Man immortal: in the transmission of his germ life and in the eternal perpetuation of his Original Thought." (p. 14.)

LECTURE II.

THE DANGERS OF THE UNSEEN.

vi. *The germ-theory of disease.*

"From observation, thought and deduction, I have concluded that earth, air and water are replete with multitudinous, infinitesimal, ever active creatures, probably many of which are too minute for our best microscopes to reveal to the sense of sight. These pigmy, insignificant-seeming and yet collectively formidable beings are everywhere at work —born in myriad numbers, propagating and expiring in a brief season, like May-Flies, e'er they hardly have begun to live; they infect or disinfect the air, alter the nature of the soil, and cleanse or contaminate the water. Entering our systems through all of these facile mediums (we inhale on an average about 2800 cubic feet of air through our lungs in the short space of only twenty four hours and swallow dust and water in surprising quantities every day of our lives) they soon obtain mastery over our weakened bodies and it is surely their malefiant effects that we behold in the horrid virulence of small-pox, the dreadful malignancy of cancer and the melancholy ravages of consumption. Kings evil, catarrh, malarial and scarlet fever, measles, the putrid sore throat, gangrene, aye, dozens of other catching ails let loose from a cursed Pandora's box among humankind, are simply the direct or indirect results of these almost invisible atoms.

"The drop of water we sip, the breath of air we breathe, the particle of dust that finds insidious entrance to our bodies, may be to us the unseen precursor of terrible disease, the unheard knell of fateful doom, the silent forerunner of early, torturing, ghastly death." (pp. 24–25.)

"...... May not soils owe their fertility or sterility, their adaptability or impracticability to the unseen workings of these Genii of the Little? May not water, also, derive many of its properties, beneficial or injurious as they may happen to be, from its teeming contents of microscopical life? We already know (from Bruce, the traveller,) that the natives of far away Abyssinia are infested with parasite Worms through the agency of the water they drink—may not many diseases of the guts originate from germs more minute than these pernicious Larvæ?" (p. 35.)

vii. *Spontaneous generation.*

"I have repeated most of these interesting experiments [of Spallanzani and Schwann] and in addition to these have made many more of my own devising. .....

"From them I find that Schwann is, in the main, correct; but further note that the close sealing he has recourse to is unnecessary, merely stuffing the mouth of the containing vessel with cotton wool will answer the same purpose; that of a germ barrier, as the most elaborate sealing if the heated wool is held in a forceps.

"A hood dipping into quicksilver answers excellently. Yet mere filtration is inadequate.

"I am now certain that this much talked of spontaneous generation is largely a delusion and that if the phenomenon ever does take place it is only exhibited under extremely unusual conditions and in most extraordinary cases. . . . . . ." (pp. 27–28.)

viii. *Cultivation from a diphtheritic throat.*

"I have placed some of the matter containing certain of what I have found to be the minute beings causing the putrid sore throat in the common calves foot jelly so familiar to all of you and covered this with a bell jar standing in quicksilver ; jelly, jar and metal all being strongly heated—thus, as you can readily understand, completely excluding any other germs. In three days, these particular germs had amazingly multiplied as rounded jointed grains in wavy clusters, and each little portion of the jelly when placed in pieces of fresh jelly was capable of plentifully propagating them in the new material which, in turn, produced them in others—and so on.

"I was curious to see how they would adapt themselves to human blood : to avoid the red color I let some venous stand quietly, having skimmed off some crust ; and drew away the greenish yellow watery serum from the cruor and heated it for some hours to 140° of Fahrenheit which I have found sufficient to destroy germ life. In this the beings appeared in only thirty hours ! and were larger, fibrous and moist. Other children in the same house with the boy from whose throat I obtained the matter, yielded none of the peculiar germs referred to—until some acquired the same disease, these then exhibited the noxious organisms in his or her greyish throat matter." (pp. 28–29.)

ix. *Contagion.*

"Reflection on this [the statements in the two paragraphs last quoted], leads us to consider how many diseases may be introduced, transmitted or conveyed by the contact of flesh, perspiration or saliva and how cautious, how prudent and how circumspect we should ever be in governing the intercourse of ourselves and of our children with other persons or creatures, no matter whether the latter appear to be clean and healthy or not. . . . . . .* " (pp. 29–30.)

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* Continues with "If the system is in proper condition", on p. 34.

x. *Resistance: Suggestions of phagocytes.*

"Only nearly perfect, very healthy, vigorous bodies can successfully resist these parasitic wanderers, (Ishmael-like roamers through the universe) when they are at their best and we are exposed to their attacks: hence we note a favored few who defy plague and pox and cholera; epidemics of all fateful kinds and remain serene, incautious and unscathed. But wo to the weak, the ailing or the debauched! they fall an easy prey to the fatal onslaughts of these tiny destroyers, everywhere watchful, voracious, insatiate; even as the Harpies of fable or the vulture that preyed on Promotheus [sic]. Why this is so, I am unable to say; it is doubtless for the same reason that a stunted, set back, or sickly plant yields to the massed attacks of aphide hosts while healthier close by vegetation of the same kind is nearly free from the vermin destroying the weaker foliage: from what either results, our too scanty store of knowledge avails us not to tell. It may be that, precisely as the spermatozoa, which Leeuwenhoek in 1677 discovered existing in the bodies of men; so other living germs, antagonistic to the evil kinds, may oppose the latter in undebilitated systems and wage war upon the humors in our blood." (pp. 25–26.)

". . . . . . If the system is in proper condition one will go as safely through any contagion as a diver in Halley's suit through the water of the sea, but who is so wise as to know when he is absolutely hale and hearty? one fatal moment of inviting weakness, and wo! the insidious germ has found a foothold.

"Then comes the difficulty of dislodgment. These creatures floating numerously through the entire atmosphere and only able to thrive in a congenial harbourage: just as the Tobacco Worm can subsist but on the foliage of the plant from which it receives its name—once having effected this subtle lodgment in our systems, are there protected by phlegmatic or viscid excretions partly emanating, perhaps, from their own organisms and partly consisting of corruption thrown out by the irritated tissues for the purpose of resisting the invasion: as observed in putrid sore throat and in catarrh; and then withstand many substances that otherwise would immediately kill them.

"Do not misunderstand me: I do not mean to say that all diseases are thus contracted, but only those that are similar to those I have mentioned. Nor do I assert that the observance of all the precautions hinted at, will ward off all danger. . . . . . .* " (pp. 30–31.)

" . . . . . . We have an approach to something of the kind in Jenner's valuable vaccine for the prevention of Small-pox. Here, I believe, is shown a striking instance of the destruction of one germ by another : the substance he employs must contain creatures antagonistical to those of the Small pox pustules, else how could its effects endure so long in the systems of those inoculated with it ? And that this, supplied in sufficient quantities, not only overwhelms those of the malady when they enter the blood, but continues to exist, inhabit and breed in that fluid thereby preventing entrance of the other and fatal germ life. If this is so, then what a Sun of Hope—Hope that should 'Spring eternal in the human breast' bursts in dazzling splendour on afflicted Man : consumption, cancer, cholera, all must mitigate, recede, or vanish before benificent germs meeting the horrible, destructive causes on their own grim ground and remaining triumphant on the never again to be fought-for field. . . . . ." (pp. 33–34.)

xi. *Insects as carriers of disease* : *Malaria and the mosquito* : *the House-fly.*

" . . . . . . Careful observation has led me to perceive that many of our common insects are conveyers of the germs of illness, disease and death. The House-Fly that crawls over our food or drowns itself in our drink, the Gnat that buries its lancet in our veins, the Bed-Bug that attacks the uncleanly during the slumbers of night, the Wasp and the Bee that thrust us with their stings—are all transporters, injectors or introducers of germ life.

" My reasons for affirming this are briefly comprised in the statement that I have never known a person to suffer from malarial fever that had not at one time or other been stung by Gnats or been the resident of a region containing these pests ; and that anyone can appreciate the too palpable filthiness of the Fly, feeding, crawling, rioting and breeding in the loathsome repulsiveness of refuse, offal, and decaying abominations of every conceivable kind ; then alighting on our victuals or on our persons to trail his defilement over our absorptive epidermis . . . . . ." (pp. 31–32.)

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* Continues with "Careful observation has led me to perceive", &c., below.

xii. *The exclusion of house-flies: the utilization of natural enemies.*

"I suggest that wooden frames be covered with metal gauze such as is used for sieves, and hinged on outside of doors and windows, otherwise, with free access to your houses, what can be safe from the Fly? . . . . How to accomplish this [the extermination of the Fly], and also annihilate the swarms of Ticks, Fleas, Gnats, Bed-Bugs and so forth, is indeed a question. Of course cleanliness will affect something towards the desired end; but, perhaps, more than this may be called into play: maybe other creatures can be bred that may abate the numbers of these vermin, just as the Mungoos is used by the Hindu to destroy the Cobra-di-Capello, as the Ferret is set upon the Rat in England and the Ladybird is said to be employed in the South of Europe to exterminate the larvæ of various insects that prey on the poor peasant's scanty crops . . . . . ." (pp. 32–33.)

The author brings his second lecture to a close in a paragraph which obliterated 40 years and made me a boy again, reading Herbert Spencer's 'Principles of Biology' for the first time.

"All this", he is alluding to his germ theory and its possibilities, "I believe will be proven to be fact, and in its darker aspect we are very naturally brought to see no hand of God. For what just, compassionate and merciful Father Diety would let loose a host of death dealing, ravenous Wolves in miniature, upon ignorant, frail, supplicating creatures of his kindly creation—his own, fore known, fore-destined, children? . . . . . ." (pp. 35–36.)

Similarly, Herbert Spencer, after describing the adaptations by which a number of parasites are enabled to wage successful war upon mankind, continues:—

"What shall we say to this arrangement? Shall we say that man, 'the head and crown of things,' was provided as a habitat for these parasites? Or shall we say that these degraded creatures, incapable of thought or enjoyment, were created that they might cause unhappiness to man? One or other of these alternatives must be chosen by those who contend that every kind of organism was separately devised by the Creator." ('Principles of Biology,' London, 1864, vol. i. pp. 343–4.)

Herbert Spencer finds the answer to his question by invoking evolution and the struggle for life as its motive cause:—

> "Slowly, but surely, evolution brings about an increasing amount of happiness: all evils being but incidental. By its essential nature, the process must everywhere produce greater fitness to the conditions of existence; be they what they may . . . . . . The universal and necessary tendency towards supremacy and multiplication of the best, applying to the organic creation as a whole as well as to each species, is ever diminishing the damage done—tends ever to maintain those most superior organisms which, in one way or other, escape the invasions of the inferior, and so tends to produce a type less liable to the invasions of the inferior. Thus the evils accompanying evolution are ever being self-eliminated. Though there may arise the question—Why could they not have been avoided? there does not arise the question—Why were they deliberately inflicted? Whatever may be thought of them, it is clear that they do not imply gratuitous malevolence." (*ibid.* pp. 354–5.)

The author of this remarkable pamphlet takes different ground in seeking for his answer. Many will think—in spite of the narrow and aggressive spirit which disfigures the passage,—that he takes higher ground. In the attacks of the germs of disease upon man he sees no hand of God, but—

> " . . . . . . rather the astonishing, strange uncomprehended workings of some mightier power in almighty Nature infinitely beyond the weak, puny, priest aborted rudiments of perception, dawning in the infant brain of Man: carrying out a grand design of unfathomable profundity, in which an atom is as mighty as a mass, a second as significant as a thousand years, and the smallest being in the universe of as much importance in the stupendous scheme as lordly Man, himself, with all his presumption, arrogance and self conceit thick upon him—leading us to exclaim with Hamlet, in immortal Shakespeare:
>
> 'There are more things in Heaven and Earth, Horatio,
> Than are dreamt of in thy philosophy!'"
>
> (p. 36.)

I do not propose, on the present occasion, to discuss the history of the ideas which have been quoted from the booklet. Any such consideration is better deferred until the authenticity of the date has been tested by every possible means. It is, however, appropriate to say at once, concerning what is perhaps the most surprising statement in the work, that it supplies no evidence that the bacillus of Diphtheria had been seen by the author. My friend Dr. F. W. Andrewes of St. Bartholomew's Hospital wrote to me May 17 & 19, 1913:—

"I should regard the term 'rounded, jointed grains in wavy clusters' as a bad description of the bacillus of Diphtheria. On the other hand the phrase would be quite apt in describing the clusters of Streptococci which would commonly be present in sore throats or even in Diphtheria itself, and the appearance is one which might be visible with an inferior microscope. I think it would be correct to say that, *by crude methods*, clumps of Streptococci would be more readily recognized in sore throats than in normal throats. The microscopist can get from a sore throat something tangible to look at, and, in most sore throats, of whatever nature, he would be likely to see clusters of Streptococci."

A curious point about the first lecture is the very inadequate criticism of Lamarck whose theory is described as founded "entirely on Spontaneous Generation" (p. 18). The same is also true of the treatment of the "Vestiges of the Natural History of Creation" (1844) alluded to in the first lecture (1847) as having "appeared about three years ago" (p. 19).

The defence of phrenology (pp. 17–18) is consistent with the date assigned to the lectures; although, from information lately received, there is no doubt that the author retained his convictions on this subject unshaken up to the end of his life.

There are curious spellings some of which are obvious misprints. Beneficent in the form of "benificent" cannot be thus explained, for it appears three times (pp. 13, 19, 34).

Life of the Author.

I am now able to give a brief account of the life of the author, received only on the morning of May 20th from his son Mr. John F. Sleeper, of Tenafly, New Jersey. The information, partly conveyed in a letter and partly in newspaper cuttings, was the outcome of letters written to four American gentlemen bearing the name Sleeper whose addresses had been given to me by Mr. B. R. Miller.

George Washington Sleeper was born in Baltimore on Oct. 15, 1826. He went to Boston as a lad and eventually opened a great tea store there and later in Providence. He was prosperous in business until he was ruined by the Civil War and by the unpopularity of views which he never hesitated to express. The dates of his residence in Boston and Providence are given in Dr. Putnam's quotations on pp. 41, 42 from the Boston and Providence directories. After leaving Providence he went to New York, residing in Jersey City, N.J., where he died on Sept. 13, 1903. He was able to recover in a measure from his misfortunes, at one time selling books, at another travelling for a New York firm. He married in 1858 and a son, Mr. John F. Sleeper, was born in 1864.

His son's letter, dated May 10, 1913, gives a graphic picture of the persecution suffered by G. W. Sleeper. His outspoken views,—prominent in the booklet which is the subject of the present address—"drew down upon him the wrath of 'the bigots of his iron time.' Undismayed, he defied them all. Clergy—government—society—relatives—all! His friends shrank away (not even his *relations* could understand him; they declared him a lunatic), his enemies prevailed, he was mobbed and assaulted in the streets and halls, his bosom friend, Hilton, pulled his beard in public, his lectures were suppressed: all that frantic malignity could do to obliterate his written and spoken thought was resorted to." These statements are supported by the preface to the booklet quoted below and on page 42. At the same time it is only fair to remember that the language of the lectures was highly provocative and aggressive, and would have been likely to produce a remarkable effect upon hearers in the middle of the last century, and indeed in much later years. The preface to a later lecture "Education and its Offspring Civilization" (Providence, 1860) speaks of the alteration of notices and attempts to efface records so as make it appear that it was never given before the "Franklin Lyceum" of Providence. The appendix to the same lecture reproduces minutes and press notices in order to prove the fact of its delivery. Apart from the far greater detail given in the later pamphlet there is a striking similarity in the description of the conditions under which both were written. In both, the expressed object of the writer is to print addresses which neither audience nor Press would receive.

THE AUTHENTICITY OF G. W. SLEEPER'S PAMPHLET (1849).

The author's conclusions on a number of extremely important subjects have been given in his own words in the first part of this address. If it be true that these conclusions were reached by 1849, the fact is of the highest interest in the history of scientific thought. The author claims indeed that his ideas were older still by several years, for he says in the introduction—

> "The original ideas on which these lectures were founded, entered my mind when I was barely seventeen, and during their gradual development the major portion of both of the lectures were committed to paper in the course of the past six years. The first public delivery of either occurred in Boston about two years ago, ..."

The above statement is consistent with the history of G. W. Sleeper, who was born on Oct. 15, 1826, and would therefore have been seventeen in 1843, six years before the date printed on the pamphlet. In 1847 he would have been twenty-one—a *very* early age, it must be admitted, for the amount of thought and reading implied by the two lectures.

Science is rightly exacting of proof when she is called upon to revise her history; and it now becomes our duty to enquire, and if possible to decide, whether these statements are true,—whether the pamphlet was printed in 1849 or at some later date. It may be admitted at once that the general appearance of the work—the paper, type and style of printing—is entirely in its favour. This is the opinion of many eminent authorities who have kindly examined it for me—of Sir Frederick Kenyon and his staff at the British Museum Library, of Mr. Madan, Bodley's Librarian, and of Sir James Murray.

The Paper.—I have submitted photographs of the watermark to Mr. Lewis Evans, who kindly wrote May 2, 1913:—

"I have been looking through two collections of watermarks that I have but can find nothing conclusive in them. I have two small undated pieces of paper of which I enclose a tracing very like the mark in the pamphlet, they are hand-made, either English or Dutch, and I should think between 1790–1850: the VI or more probably I.V is not an uncommon mark, but whether it stands for 6, 4 or I. Van—— I do not know. The pamphlet paper is I fancy Dutch and I think it would be made before 1849, but I do not know how far Dutch paper was in general use in U.S.A. about that date. The shield with 3 lines across it is fairly common in Dutch papers."

Mr. G. A. James Rothney also kindly wrote from John Dickinson & Co., London, April 30, 1913:—

"We have found a letter from the East India House, Leadenhall St., dated 5th Oct. '55, which has a watermark identical with the size mark, but it has no Roman lettering IV.

Mr. Johns—our great paper expert—rather fancies it is a Dutch handmade."

The Type.—Mr. Horace Hart, controller of the Oxford University Press, has kindly examined the type for me. The words "Some Recent Lectures" on the title-page and cover are almost identical with a line of "two-line Small Pica ornamented Latin" in a trade catalogue issued by the late firm of V. & J. Figgins. The catalogue was undated, but an order form with the decade "188–" was bound into it. "The Origin of Life" (p. 1) and "The Dangers of the Unseen" (p. 20) are almost identical with "two-line Brevier Monastic No. 2" in the same catalogue. It is certain that this type in the pamphlet was copied from that of Messrs. Figgins or *vice versa.* I applied to R. H. Stevens & Co., successors to V. & J. Figgins, but was unable to learn the date. Messrs. Stevens wrote Apr. 22, 1913:—"The two Faces that you mention are quite old and out-of-date, and we have no record of the date when they were first made."

Mr. Hart has written to me, May 23, 1913, on the questions raised in the preceding paragraph:—"I think you may take it as conclusive that the American founder would follow the English founder and not the other way about. You may also take it for granted that the typefounding firms would continue issuing their old types for a great many years. It is a question of fashion rather than anything else. The types that you are interested in have gone out of fashion, and that is the reason why they do not appear in the typefounders' specimen books to-day. There are, of course, people who have made a study of types and their dates; but it happens that the types we have been discussing, are what are called Jobbing or Display types, used for circulars and advertisements; and no one is particularly interested in them.

"My opinion about the little booklet which you showed to me is, that it was not only set up, but was also printed off, and done up, *i. e.* stitched and put into its cover, by an amateur printer, and not by a regular printer. And it might very well have been printed in Boston at the date mentioned."

Mr. Hart also told me when I showed him the pamphlet a few weeks ago that the paper had not been damped, and that this and the setting-up, inking, and black marks made by the "furniture" showed that the work had not been done by a printer, but by an amateur who had access to a press of fair size. In all these respects the pamphlet presents an appearance remarkably different from the author's lecture, "Shall we have Free Speech?" undoubtedly printed in 1860—only eleven years later.

It is perhaps worth recording that the two titles appear to have been set up from a very small stock. The Brevier Monastic "i" is without a dot, but this feature is only wanting from the two letters in "Origin": the "i" in "Life" has been printed from a letter of another fount turned upside down, so that the dot is below the line.

INTERNAL EVIDENCE.

Registration and Press notices.—The first and most important line of evidence breaks down. The following words are printed on the back of the title-page: "Entered according to Act of Congress, in the year 1849, by Geo. W. Sleeper, in the Clerk's office of the District Court of Massachusetts." My friend Prof. C. S. Minot of the Harvard University Medical School has kindly written for me to Dr. H. Putnam of the Library of Congress, Washington, who states, Apr. 30, 1913:—"The Register of Copyrights reports that the copyright records for Massachusetts for the year 1849 are in his office and have been examined page by page, without discovering the registration of this work." Prof. Minot, however, writes, May 9, 1913:—"The record of copyrights begins with 1846, and I understand that the records for a few years are considered not to be perfect, so that there is a possibility of Sleeper's pamphlet having been issued and copyrighted, as stated on its title-page. It is, however, extremely improbable that such was the case." Further evidence by Dr. Putnam is more positive:—"We find the names of both the author and printer in the Boston directory for 1849. Sleeper's name also appears in the Boston directory from 1849–1855 inclusive; then in the Providence directory from 1856–1865, in both places his occupation is given as a tea merchant. His name again appears in the Boston directory from 1866–1872 *. Here he is listed as a printer. . . . . . From the above it appears that the author and printer of the pamphlet lived in Boston at the time of the publication of it, thus affording evidence of its genuineness. The only negative testimony is that the copyright records of Massachusetts for 1849, which are in the custody of the Register of Copyrights, fail to show that the book was copyrighted as claimed."

The statement of registration is in favour of the authenticity of the work; for it is unlikely that one who was forging a date would print a conspicuous paragraph by which the forgery could be so easily detected.

The attempt to find evidence in the Press of the delivery of the lectures in 1847 or the publication of the work in 1849 has also failed. Mr. Horace G. Wadlin, Librarian of the Boston Public Library, has kindly written, Apr. 23, 1913:—"An exhausitve search of Boston daily newspapers for 1846 and 1847 . . . . . has failed to reveal any information concerning G. W. Sleeper." Dr. Putnam writes:—"Search has also been made in the files of some of the Boston newspapers of that period [1849], but without avail. This search is not quite completed and if we should discover it I will inform you." Supposing that the pamphlet is genuine the remainder of the introduction, of which the first portion was quoted on p. 39, gives an explanation of the silence of the Boston Press.

> ". . . . . . The first public delivery of either occurred in Boston about two years ago, it was, however, almost impossible to obtain a hearing for them so bitterly hostile did the audiences (assemblies little better than savages) prove themselves to be, and so persistently did they interrupt, and endeavor to overawe, the lecturer.
>
> "Such being the condition of society, and as the press of this city, influenced by certain clergymen, have not seen fit to acquaint the public either with the substance of the ideas set forth or with the facts relating to the attempts to deliver the lectures containing them, I decided to put these subjects to print; as being the only way open to secure attention from the many fair and noble minds among our citizens who undoubtedly have Common Sense."

Comparison between G. W. Sleeper's pamphlets of 1849 *and* 1860.—We know that the date (Providence; 1860) of the later pamphlet, "Shall we have Free Speech?" is genuine; for the copy in the British Museum Library bears the stamp "June 9, 1864." This work is stated to be registered in "The District Court of Rhode Island," and I have asked Dr. Putnam if he will kindly ascertain whether it is actually entered in the records of the Court *.

---

* Mr. J. F. Sleeper informs me that this is an error and that his father did not return to Boston but went to New York in June 1866.

The comparison between the two pamphlets is, in my opinion, unfavourable to the authenticity of the one with the earlier date. The undoubtedly genuine pamphlet contains nothing surprising, nothing that any able man, well read in the ethnology of his day, might not have inferred. Although the two works present obvious resemblances—for instance in the treatment of gunpowder—there is not the slightest hint in the later pamphlet of the existence of the earlier one, nor of any original view contained in it. And there is one passage at least where such reference was to be expected. Speaking in 1860 of the unsanitary conditions of ancient Greece the author says:—"Undoubtedly these tended to cause the great plague of Athens—which unheard of disease in modern times is no doubt owing to the superior education of man, whose vast accumulation of scientific facts are fast developing the origin and causes of great pestilences." (p. 13.)

History of the only copy at present known †.—By far the strongest evidence in favour of the authenticity of the earlier work is to be found in the history of the copy now presented to the Society, as given in the first part of this address (pp. 26–27). Many of the ideas *must* have been originated by the author, if they are printed in a pamphlet bought in 1891 or 1892 of a bookseller who then said that it was an old work and had been through many hands. This history destroys the validity of an objection which has been felt by many to whom I have shown the pamphlet—the very completeness and balance of the anticipations, and the fact that so many important modern ideas are touched off, often in a few lines. The views on the origin of life and on insects as carriers of disease must I think, under any circumstances, have been original, and those upon the germinal origin of characters and some of the thoughts on resistance almost certainly so.

The excessive rarity of the pamphlet is probably a point in favour of its authenticity.

The use of characteristic Huxleyan and Spencerian words.—When I read the pamphlet for the first time, I was struck with the employment of the word "Agnostic" as though it were in general use. The author is speaking, on page 15, of Education and what she has done for Man. He speaks of "her Commerce and Travels; her Printing Press and Schools; her Gunpowder and her Agnostic with his untrammelled thought, ...".

"Unknown Cause" on p. 5 and "vegetal" on p. 2 (we find "vegetable" on pages 9 and 19) suggest Herbert Spencer, but

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* Dr. Putnam has now kindly sent me a letter from Mr. Thorvald Solberg, Register of Copyrights, stating that the title of the 1860 pamphlet was duly registered on April 27, 1860, but that no copy was deposited.—E. B. P. Aug. 12, 1913.

† I have since learnt from Mr. J. F. Sleeper that he possesses three copies of the pamphlet.—E. B. P. Aug. 12, 1913.

Sir James Murray informs me that "vegetal" is very old, going back even to Caxton (1490).

Huxley's creation of the word "agnostic" in 1869 is well known, but I think it will be of interest to quote the passages from the "Life and Letters" (London, 1900, vol. i. pp. 319, 320). Under the year 1869 we read:—

"...... How he came to enrich the English language with the name "Agnostic" is explained in his article "Agnosticism" (Coll. Ess. v. pp. 237–239).

"After describing how it came about that his mind 'steadily gravitated towards the conclusions of Hume and Kant,' so well stated by the latter as follows:—

> 'The greatest and perhaps the sole use of all philosophy of pure reason is, after all, merely negative, since it serves not as an organon for the enlargement (of knowledge), but as a discipline for its delimitation; and, instead of discovering truth, has only the modest merit of preventing error':—

"he proceeds—

> 'When I reached intellectual maturity, and began to ask myself whether I was an atheist, a theist, or a pantheist; a materialist or an idealist; a Christian or a freethinker; I found that the more I learned and reflected, the less ready was the answer; until, at last, I came to the conclusion that I had neither art nor part with any of these denominations, except the last. The one thing in which most of these good people were agreed was the one thing in which I differed from them. They were quite sure they had attained a certain "gnosis"—had, more or less successfully, solved the problem of existence; while I was quite sure I had not, and had a pretty strong conviction that the problem was insoluble. And, with Hume and Kant on my side, I could not think myself presumptuous in holding fast by that opinion ......
>
> 'This was my situation when I had the good fortune to find a place among the members of that remarkable confraternity of antagonists, long since deceased, but of green and pious memory, the Metaphysical Society. Every variety of philosophical and theological opinion was represented there, and expressed itself with entire openness; most of my colleagues were *-ists* of one sort or another; and, however kind and friendly they might be, I, the man without a rag of a label to cover himself with, could not fail to have some of the uneasy feelings which must have beset the historical fox when, after leaving the trap in which his tail remained, he presented himself to his normally elongated companions. So I took thought, and invented what I conceived to be the appropriate title of "agnostic." It came into my head as suggestively antithetic to the "gnostic" of Church history, who professed to know so much about the very things of which I was ignorant; and I took the earliest opportunity of parading it at our Society, to show that I, too, had a tail, like the other foxes. To my great satisfaction, the term took; and when the *Spectator* had stood godfather to it, any suspicion in the minds of respectable people that a knowledge of its parentage might have awakened was, of course, completely lulled.'"

The following account of the origin of "Agnostic" is given in the great Oxford Dictionary:—

"Suggested by Prof. Huxley at a party held previous to the formation of the now defunct Metaphysical Society, at Mr. James Knowles's house on Clapham Common, one evening in 1869, in my hearing. He took it from St. Paul's mention of the altar to 'the Unknown God.' R. H. Hutton in letter 13 Mar. 1881."

Sir James Murray informs me that no importance can be attached to "clewless" (p. 5) of which the first quotation (in the form of "cleuless") is dated 1862 in the Oxford Dictionary.

At this point I must leave the problem, hoping to be able to add in an appendix or in an early communication to the Society the evidence which will enable us to reach a decisive conclusion.

[Since the delivery of the above address I have been in continual communication with Mr. John F. Sleeper, who has kindly permitted me to see much interesting manuscript with a direct bearing on the authenticity of the pamphlet. The new facts suggest further enquiries which are being undertaken but cannot be hurried. I therefore leave the address as it was delivered, save for a few necessary corrections and occasional notes, the latter with the date Aug. 12, 1913. The results will be communicated to the Society at the earliest possible date.

E. B. Poulton, Aug. 13, 1913.]

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[*Extracted from the* Proceedings *of the* Linnean Society
of London, Session 1913–14.]

CONTINUED INVESTIGATIONS INTO A REMARKABLE AMERICAN WORK UPON EVOLUTION AND THE GERM THEORY OF DISEASE.

THE PRESIDENTIAL ADDRESS
READ BEFORE THE
LINNEAN SOCIETY OF LONDON
AT THE
ANNIVERSARY MEETING,
May 25, 1914.

BY

Professor EDWARD B. POULTON.

LONDON:
PRINTED BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.
1914.

PRESIDENTIAL ADDRESS, 1914.

WHEN I had the pleasure of addressing you on May 24, 1913, I little thought that the same subject would require another year's intermittent work, and furnish the material for another Anniversary Address. But G. W. Sleeper's booklet, dated 1849, had been in my hands only two months, and the enquiry was still proceeding, when the address was delivered. I had informed the author's son, Mr. J. F. Sleeper, that the registration of the work was not to be found among the copyright records for Massachusetts for the year 1849, that there was no evidence of a copy having been deposited, and that therefore any documentary proofs which he could furnish would be of the utmost importance. His reply, which arrived on June 2nd, a few days after the delivery of the Address, shewed that decisive evidence was in his possession:—

> Bense's contract, signed and sealed by him and dated May 18, 1849, is among my father's papers; there is an entry in his old memo book for 1849, "Bense, pamphlets, $30," under that date; and an MS. lecture, "Life and the Cosmosite," refers to the Origin of Life as delivered in 1847.

Mr. J. F. Sleeper had previously stated that the word "Agnostic" had been introduced by his father, and that it was to be found in the manuscript of a lecture to which he assigned the date 1846.

I wrote asking for the loan of all these documents, in order that they might be examined by experts. Mr. Sleeper replied that, in the absence of the expected registration, they had become so precious that he could only submit them one at a time, and could only despatch the second after the safe return of the first, and so with the rest. This meant loss of time; but the perfectly reasonable conditions could not be resisted, and I still hoped that expert opinion would be unanimous, no further evidence required, and the whole subject brought to a decisive conclusion in a terminal note to the 1913 Address. With this hope, the revised proofs were held back from the press until late in the summer; but by August 13 it was obvious that the enquiry was far from complete, and I therefore returned the proofs to the General Secretary, after adding the brief explanatory paragraph on p. 45.

I fully expected when the proofs were returned that the investigation would be finished in time for a meeting in the autumn session; but, partly because I could not devote myself to this subject continuously, although mainly on account of the inherent difficulty of pursuing enquiries in another and distant land, it was soon realised that many months must elapse.

The necessary delay has been of special and great advantage, in that it has afforded the opportunity for settling, as I believe finally, the date of certain type used in printing the booklet—a problem which last year appeared to be insoluble.

I do not think that the Fellows of the Linnean Society will criticise too severely the devotion of two Anniversary Addresses to this interesting subject. Had I not seen, in the documentary evidence and the lines of enquiry suggested by it, the probability of a final decisive solution, I should not have hesitated to express my own conclusions as to the authenticity or otherwise of the booklet; although it is not to be expected that the opinion would have received universal or even general approval. On the evidence available a year ago, many thinkers held that the booklet was the outcome of remarkable genius, many that it was the product of remarkable fraud. Whether genius or fraud, it is certainly remarkable, as I fully realised when the title of the address was deliberately chosen:—“A remarkable American Work upon Evolution and the Germ Theory of Disease.”

The evidence now brought forward will probably lead the scientific and literary world to an undisputed conclusion—that the work is a fraud; but, when the story is told, I do not doubt that the word “remarkable” will, by general agreement, be allowed to stand.

Much kind help has been received in the course of the investigation, which, indeed, could not otherwise have been carried to a successful issue. All such help is acknowledged in the course of the Address, but I must at the outset specially record my grateful thanks to Mr. Horace Hart, Controller of the Oxford University Press; Mr. J. W. Phinney, Manager of the American Typefounders' Company, Boston, Massachusetts; Sir George Warner, late Keeper of the Manuscripts of the British Museum; Mrs. Frederic Endicott, of Canton, Massachusetts, a daughter of the late Mr. W. Bense; Dr. H. Putnam, Librarian of Congress, Washington; Mr. H. G. Wadlin, Librarian of the Public Library, Boston.

I also desire to thank Mr. F. Madan, Bodley's Librarian, Oxford University, for his great kindness in correcting the proofs of the reproduction in the Appendix, comparing them line for line and word for word with the original booklet. Fellows of the Linnean Society owe to his kindness, and to the skill of the experts of the Oxford University Press, that they will possess an exact reproduction in all essentials of the work stated to be written by G. W. Sleeper and dated 1849.

Mr. J. F. Sleeper has been most kind in supplying documents and answering questions, and I fear that the long correspondence has absorbed much of his time. I regret that I have not been able to accept his conclusions. On p. 44 I have ventured to suggest the mental condition which led to the fabrication of evidence. The solution offered—that of self-deception—is, I hope, not only the correct one, but also the one which will bring the least distress to my courteous correspondent.

1. *The Type.*

At the time when the revised address for 1913 was sent to press, no clear evidence based on the type had been forthcoming (Proc. Linn. Soc. 1912–13, pp. 40, 41). Some of the founts had been found by Mr. Horace Hart in an undated catalogue of V. and J. Figgins, but their successors had been unable to trace the history. Mr. Hart, on the whole, concluded that the booklet "might very well have been printed in Boston at the date mentioned" (p. 41).

The enquiry has now been carried much further, and has produced results of the highest importance. On July 16, 1913, Mr. Hart wrote the following letter to his friend, the late Mr. Theodore L. De Vinne, of 300 West Seventy-sixth Street, New York:—

> I am troubling you with a question about the date of certain types, which will interest you, especially if you are able to make the necessary references to typefounders' catalogues in your own possession.
>
> I have a pamphlet, the titlepage of which is as follows:—
>
> SOME RECENT LECTURES.
> By GEO. W. SLEEPER.
> Boston: Wm. Bense, Printer, 1849.
>
> I have been assisting . . . . . . to fix the date by means of the types, and I have chosen three founts as tests. These are:
>
> (1) Type used for certain headings: Figgins's two-line long primer Monastic No. 2.
> (2) Ditto. : two-line brevier Monastic No. 2.
> (3) Ditto. : two-line small pica wide Latin.
>
> The point I would submit to you is,—Can you say with any certainty that 1, 2, or 3 existed in America as early as 1849? I find them in late editions of Figgins's Specimen Books; but unfortunately their business has been sold to Messrs. R. H. Stevens & Co., and the new firm has not the means of finding out anything about origins of types.
>
> I have not found these types in your specimen books.
>
> P.S.—On second thoughts, I am sending you a couple of rotographs, one of the titlepage which contains the types I am writing about, and the other containing a drive-down * heading. The words "SOME RECENT LECTURES" are in the wide Latin type, and the words "The Origin of Life" are in the two-line long primer and brevier Monastic No. 2.

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* A heading that is not printed at the very top of a page, but is driven down, as at the beginning of any important section of a book.

Mr. De Vinne, in acknowledging the receipt of this communication, said he was getting old and could not himself undertake the necessary research, but that he had handed Mr. Hart's letter and enclosures over to Mr. J. W. Phinney, the Manager of the American Typefounders' Company, Boston. Mr. Phinney kindly undertook a thorough investigation, which occupied some months, and it was not till Nov. 4, 1913, that Mr. Hart received the following reply :—

> Mr. Theodore L. De Vinne has handed me your inquiry about the date of certain types used in the titlepage of a pamphlet entitled "Some Recent Lectures by George W. Sleeper; Boston, William Bense, Printer, 1849."
>
> I have examined my specimen books of French, German, English, and American types, and am disappointed.
>
> Our Librarian in Jersey City, where we have a Typographic Library and Museum, has examined the catalogues of four Libraries, and is unable to find the Sleeper Lectures pamphlet.
>
> The type has been variously called "Norman," "Wide Latin," "Celtic No. 2,' etc.
>
> We do not find any specimens of "Norman" in French specimen-books earlier than 1879, in Berthier, a concern with a reputation of [producing] faces foreign to France. Even at this day no French specimen-book of a leading type-foundry shows "Norman." The earliest showing in England was by Figgins, 1873, one size, two-line Great Primer, Caps. and Small Caps., called "Wide Latin." The same book shows "Ornamented Latin," three sizes, with Floriated Caps. and Small Caps. similar to "Wide Latin," in bodies corresponding to our 6-, 8-, 10-, 12-, and 18-point sizes.
>
> Figgins also shows the Floriated Caps. separately under the name "Latin Initials."
>
> We have not been able to find the face in German books earlier than 1885.
>
> MacKellar, Smiths, & Jordan's 'Typographic Advertiser' of July, 1870, shows the face in eight sizes as "Celtic No. 2." All other specimens in that issue are priced, indicating that the face was quite new at that date in that foundry.
>
> The Matrix Book of the Johnson Foundry shows that the face was first added in 1870. The matrices are electrotyped. The specimen has no patent date, while all faces originating in that foundry were patented as they appeared.
>
> Conner's 'Typographic Messenger' shows the face in 1873, as a supplement, printed on one side, suggesting that it was just added.
>
> The Boston Type Foundry shows the face in five sizes of Caps. in 1874, and there is a note to the effect that "Small Caps. are in preparation."
>
> Our collection has the Dickinson book of January 1876, in which "Norman" is shown in four sizes in Caps. and Small Caps. I believe the Dickinson commenced to manufacture the "Norman" in 1874.

Finally, in a letter written March 16, 1914, kindly giving me permission to quote the above statement, Mr. Phinney summed up the results of his enquiry in these words :— "It seems to me impossible that the titlepage could have been set at the date claimed for it, the style of type used in some of the lines of the titlepage being designed at a much later date, as we have recently established in the running-down we gave to the type face."

2. *Early Workmanship of W. Bense compared with that of the Booklet dated* 1849.

The rough appearance of the booklet was referred to in last year's address (p. 41), where Mr. Hart's opinion that it was the work of an amateur is quoted, and where it is compared unfavourably with the 1860 pamphlet.

Sir George Warner wrote, August 7, 1913, after seeing the booklet:—

> Apart from its really astonishing anticipation of modern theories and discoveries, the only thing at all suspicious about the pamphlet is that it looks almost too early and scrubby—in short, overdone, especially as it purports to have been printed at Boston, which was not a primitive Western town, but the literary centre of the States. Even if Bense was merely a printer in a small way of business, one would have expected something better, and it is a pity more of his work is not available for comparison.

It has, fortunately, been possible to supply this want; for Mrs. Endicott, a daughter of the late Mr. W. Bense, kindly sent to me on Nov. 4, 1913, two samples of her father's work set up within a few years of 1849. One is the 'Annual Report of the Selectmen of the Town of Canton' (1855); the other the 'Massapoag Journal and Canton Observer' (vol. i. No. 12, Oct. 9, 1852). Mr. Hart has kindly examined both of them, and tells me that the type referred to on p. 25 is not to be found in either, although the journal is rich in the variety of its founts. The workmanship of both is creditable, and bears no resemblance to the rough and untidy print of the booklet. The comparison affords strong evidence that the booklet was not printed by Bense.

Mrs. Endicott wrote in the accompanying letter:—

> My father thoroughly understood his business, and took pride and pleasure in it. He served an apprenticeship in the old-fashioned way with the well-established firm of Crocker and Brewster, continued with them afterward as a journeyman, and ever since my earliest recollection had his own printing-office in Boston, and I suppose was in business for himself at the time of his marriage. He must have had a proper outfit, too, for he made a specialty of dainty work, dance orders, bills of fare for some of the large city hotels, and other work of that nature.

Mr. Phinney, in his letter to Mr. Hart (p. 26), also stated that "William Bense was an excellent printer."

The copy of the 'Massapoag Journal' supplies evidence that there were business relationships between W. Bense and G. W. Sleeper; for it contains a rather extensive advertisement of the latter's "New England Tea Hong," at 130 Washington Street. Furthermore, the last advertisement in the paper, that of the printer, W. Bense, states that "orders may be left with E. & N. Bent, at the Depot, or at 130 Washington Street, Over New England Tea Hong, Boston."

Mr. J. F. Sleeper states that his father specially arranged for W. Bense to procure the paper and type from abroad, and would not permit the printer to damp the paper. No such stipulations appear in the very elaborate contract (see p. 32). The price, moreover, of 30 dollars for 500 copies, does not seem to leave much margin to pay for the special importation of paper and type.

3. *Evidence that G. W. Sleeper was described as a Printer between* 1866 *and* 1872.

In last year's Anniversary Address it is stated (p. 42), on the authority of Dr. H. Putnam, that G. W. Sleeper's name appears as a printer in the Boston Directories from 1866–1872. Mr. J. F. Sleeper, on the contrary, strongly asserted (*l. c.*, footnote) that the information was erroneous, and that his father went to New York in June 1866. I therefore asked Dr. Putnam if he would give me the precise addresses printed in the volumes. He kindly replied as follows:—

Office of the Librarian of Congress,
November 14, 1913.

The following entries occur in the Boston City Directories for the years 1866 to 1872:

1866. Sleeper, George, printer, boards 89 Hudson.
1867. Sleeper, George, printer, boards 12 Piedmont.
1868. Sleeper, George, printer, 120 Wash. b. 11 Suffolk-pl.
1869. Sleeper, George W., printer, 118 Wash. b. 29 Harvard.
1870. Sleeper, George W., printer, 118 Wash. b. 29 Harvard.
1871. Sleeper, George W., printer, 118 Wash. b. 29 Harvard.
1872. Sleeper, George W., printer, boards 10 Decatur.

It will be seen that two of the business addresses are very near that of the "New England Tea Hong," at 130 Washington Street.

Mr. J. F. Sleeper states emphatically that his father "never was a printer; any such statement in a Boston Directory for 1860, &c., is either a gross error or refers to some other person. Your proof said '1866–1872.' At that time father was in New York and New Jersey!" Mr. Sleeper also suggests many directions in which enquiries may be expected to yield confirmatory evidence. These I have not had time to make. Furthermore, any amount of evidence that G. W. Sleeper was resident in New York and New Jersey between 1866 and 1872 would not disprove his residence in Boston for portions of the same years. The proof that is required by Mr. J. F. Sleeper must deal with the Boston record. No other will suffice.

4. *The Contract with the Printer.*

The contract, of which a reduced facsimile appears opposite p. 32, is the most important document relating to the 1849 booklet that I have received. It supplies a crucial test. If it be genuine, the booklet receives sufficient confirmation, and will be accepted by the reasonable critic. If it be proved a forgery, the reasonable critic will conclude that the booklet is a forgery also.

Several eminent authorities in Oxford to whom I shewed the contract were quite satisfied with its appearance, and were prepared to accept the booklet on its authority. I do not think that any of them examined it very critically, for they appeared to be satisfied with the inherent improbability that it had been forged. Mr. Horace Hart remarked that the deed was unnecessarily pompous and elaborate for so small a sum as thirty dollars.

After receiving several favourable reports, I took the document to the Regius Professor of Modern History, Prof. C. H. Firth, who at once expressed his disbelief in it, telling me that he would not think of accepting historical data on such evidence. He did not consider that the brown stains looked genuine, and thought that the effect had been in part produced by rubbing.

Mr. J. F. Sleeper states that the lecture containing the word "Agnostic" (App. p. 15) and some other manuscripts, being crumpled and dirty, he damped them slightly with a nearly dry sponge, and then ironed them flat. Such treatment might have caused the appearance noticed by Professor Firth.

The document was then sent to Sir Frederick Kenyon, who kindly expressed his opinion as follows :—

British Museum,
London, W.C.
July 25, 1913.

I return the contract. I can't say I like the look of it. The brown stain does not look natural; it has more the appearance of the coffee-stain which one sees on faked documents than the genuine foxing. Otherwise there is not much to take hold of, though I should have expected more wear at the cracks of the folds. On the whole, though I should not like to pronounce decisively, this document rather increases my distrust than otherwise.

I have shown it to the present Keeper of MSS., who concurs; unfortunately we no longer have Warner available, whose experience is much greater than ours.

I next sent the contract to Sir George Warner, late Keeper of the Manuscripts of the British Museum, who was then at Llandrindod Wells. He kindly replied, Aug. 1, 1913 :—

I have carefully examined the document which you have sent me, but without further evidence cannot come to a positive conclusion respecting its genuineness. So far as its general appearance goes, it certainly *might* date from 1849, but I am by no means convinced that it really does so, for there is much in it that is decidedly suspicious. The discoloration (which in forgeries is so often a weak point) does not look quite natural, and I see no signs that it is caused by the use of pounce instead of blotting-paper*. But, apart from this, there seems to be an occasional tendency to lapse into what may be the writer's own customary hand as distinct from an artificial one. Take, for instance, the "∂" at the end of "aforsaid." This was originally written as "∂," but has been painfully altered to "*d*" so as to conform to the usage elsewhere; and the same is apparently the case with the "*d*" at the end of "counted." In my experience there is no letter, especially when at the end of a word, in which a forger is more often taken off his guard; and throughout the document the *d*-form seems to be made with more or less of an effort, as if the writer was not accustomed to it. I am also inclined to think that the attestation was written by the same hand as the body of the document. The mode of connecting the letter *s* with *e* or another letter following is somewhat peculiar and characteristic, and it is exactly the same in "presence" and "Joseph" as it is in "presents" (l. 1) and elsewhere †.

A few weeks after the receipt of the above letter, Mr. J. F. Sleeper kindly sent several sheets of his father's manuscript, written within a few years of 1849. These were submitted, together with a collotype of the contract, to Sir George Warner, who wrote, Aug. 28, 1913, as follows :—

> The more I see of the contract the less I am disposed to believe in its authenticity, for the hand varies too much in so short a document written all at one time to be the writer's own natural hand, and has all the signs of an attempt to disguise it. The paper, so far as I remember it, seems to be the same as that used for most of the documents now sent, but of course it may have been a blank page torn off for the purpose of the forgery, if it is one, as I more and more strongly suspect is the case. I certainly would not commit myself to a belief in the pamphlet until more copies with authenticated dates of acquisition are forthcoming.

It was obvious, after learning Sir George Warner's opinion, that every attempt should be made to obtain signatures for comparison with the contract, as well as other possible confirmation. On Aug. 9 I wrote to the Librarian of the Boston Public Library, asking if he could kindly give me the names and addresses of

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* Mr. J. F. Sleeper sent me samples of his father's white and also of his dark blotting-sand, but they bore no resemblance to the fine white powder which was thickly encrusted on some of the ink.

† Sir George also wrote on the same subject, Aug. 7, 1913 :—

In the contract it is not the similarity of the signature of Bense to the body of the document which struck me as a little suspicious, for I think there can be no doubt that, as would be natural, they were both written by the same hand. The question is, whether the signature of the witness was not also written by the same hand, though the intention was to disguise it.

These of course are only grounds for suspicion, and not proofs, but they make me very anxious to see specimens of both Sleeper's and Bense's handwriting, if it is possible to obtain them. The problem presented by the pamphlet is an extremely interesting one, and it is well to sift the matter thoroughly. . . . . The use of the term "Agnostic" staggers me, and I confess I am sceptical and disposed to ask for more proof than this doubtful contract that the pamphlet is anything more than a fraud prompted by an old man's vanity and desire to score off his detractors.

W. Bense's children. The Assistant-Librarian, Mr. Otto Fleischner, kindly replied, Aug. 22, sending the addresses of two daughters and a son. I wrote at once to Mrs. Frederick Endicott, of 1032 Washington Street, Canton, Massachusetts, who replied most kindly on Sept. 21st, and has since continued, in consultation with other members of her family, to assist the investigation. Mrs. Endicott's letter showed that no evidence was to be expected from the business books and papers that must have been kept at her father's printing establishment, for

> in the panic and confusion of the great Boston fire in 1872, the chief of the fire department ordered the blowing up of numerous buildings, among them the one at 35 Congress St., where his office was. The fire did not reach the spot, but the great building was totally wrecked, and father's finely equipped office, presses, and everything, went down in the ruins. So of course everything, books, papers, and all were gone, and he had to make an entirely new beginning.

Mrs. Endicott had never heard of Mr. Joseph Crafts, and other attempts to trace the witness to the contract have also ended in failure. Enclosed in Mrs. Endicott's letter was the signature of William Bense, reproduced on a slightly smaller scale below. The signature was the receipt for a bill dated Jan. 8, 1890, from the office at 35 Congress Street, Monks Building:—

William Bense

The signature was obviously closely similar to that upon the contract (opposite p. 32). I sent it to Sir George Warner, together with a collotype reproduction of the contract, and wrote to Mrs. Endicott begging for more signatures, especially of an earlier date, and one as near as possible to 1849. Sir George replied, Oct. 6, 1913, as follows:—

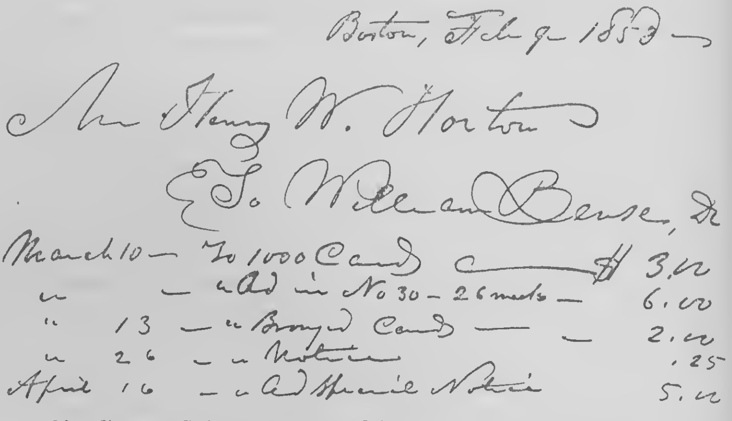
> The signature you have sent me certainly does support the genuineness of the Sleeper-Bense contract of 1849. At the same time I am not quite satisfied, for it seems to me very remarkable that after so long an interval as 40 years the signature should be so precisely identical; and it is almost easier to believe that the early one is a forgery from a considerably later example. Is there no signature of Bense more nearly of the same date as the contract?—and other writing as well, for it is the text of the contract which looks so suspiciously irregular and artificial. The signature, I think, would not be a difficult one to forge.

The hoped-for signatures, three in number, were found by Mrs. Endicott and her sister, and sent Nov. 4, 1913. One of them, reproduced in a slightly smaller size below, is of late date, Sept. 5, 1882. It is a receipt from the same office as the signature last-mentioned, and, like it, obviously resembles the one appended to the contract:—

William Bense

The two other signatures are of great importance, being much earlier—the first, of Dec. 17, 1856, not eight years, the second not quite nine years, from the date of the contract; yet both are very different from the signature on the latter. The first, the receipt on a bill, is shewn slightly reduced; the second, on an unreceipted bill, is of about half the original size, and includes with the signature the upper third of the document, so that the ordinary handwriting, as well as the signature, may be compared with the contract:—

William Bense



Boston, Feb 9 1858 —

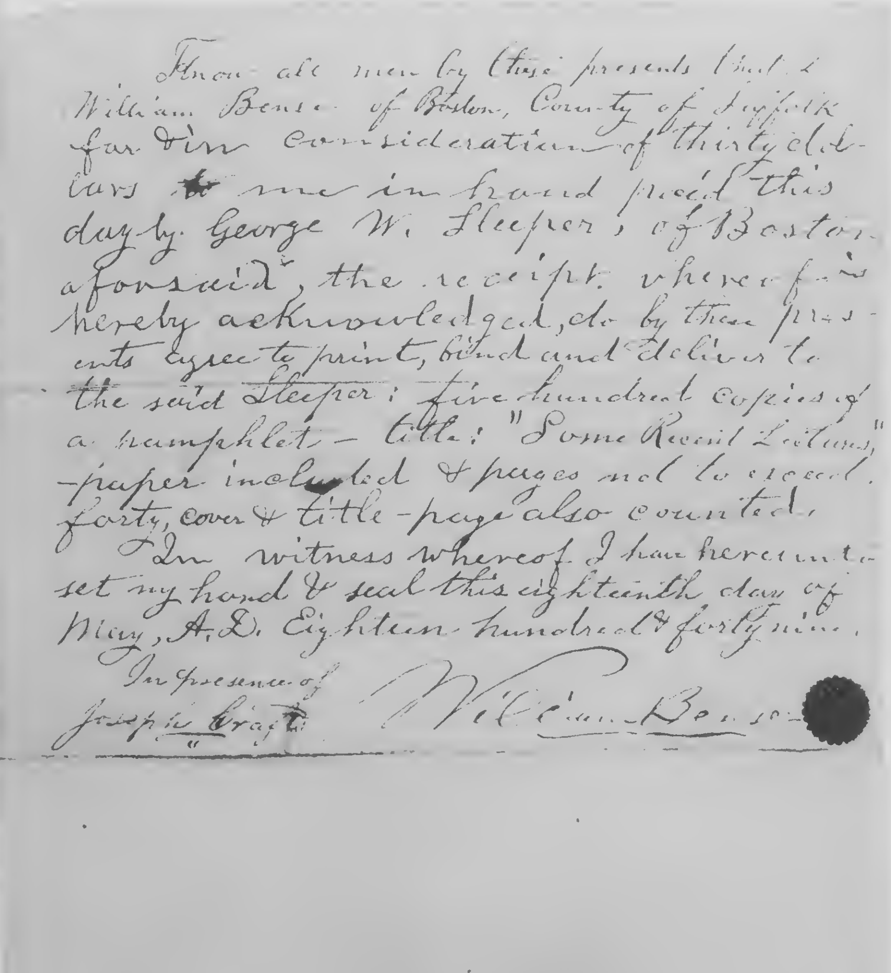
Mr Henry W. Horton

To William Bense, Dr

March	10	— To 1000 Cards —	$ 3.00
"		— " Ad in No 30 – 26 weeks —	6.00
"	13	— " Bronzed Cards — —	2.00
"	26	— " Notice	.25
April	16	— " Ad Special Notice	5.00

Sir George Warner wrote, Nov. 17, after receiving the four signatures and the collotype of the contract:—

> I have received your five documents and have compared them. The two dated in 1856 and 1858 supply the evidence which has hitherto been lacking, and I am now convinced that the contract purporting to be dated 18 May, 1849, is nothing more than a forgery, as I have suspected all along. Both the text and signature were evidently written by the same person; but the hand of the text has no resemblance to that of the items in the bill of 1858, nor



Know all men by these presents that I William Benson of Boston, County of Suffolk for & in consideration of thirty dollars to me in hand paid this day by George W. Sleeper, of Boston aforsaid, the receipt whereof is hereby acknowledged, do by these presents agree to print, bind and deliver to the said Sleeper, five hundred copies of a pamphlet — title: "Some Recent Lectures," — paper included & pages not to exceed forty, cover & title-page also counted.

In witness whereof I have hereunto set my hand & seal this eighteenth day of May, A.D. Eighteen hundred & forty nine.

In presence of
Joseph Craft

William Benson

REDUCED COLLOTYPE FACSIMILE

Size of original sheet 9 9/10 in. × 8 1/10 in.

could the latter, I think, have been developed from it, while the signature appears to have been copied from a genuine signature of Bense later, and probably much later, than 1858, after he had ceased to make the exaggerated flourish at the end of B.

I am going up to the British Museum on Wednesday and will show the documents, if I may, to Mr. Gilson and get his opinion.

Two days later, Nov. 19, Sir George wrote :—

I return the documents, which I have shown to Mr. Gilson, Keeper of MSS. at the British Museum. He agrees with me that the contract is spurious.

5. *Advertisements for the Booklet dated* 1849.

In the course of a letter written Aug. 7, 1913, Sir George Warner had made the following suggestions :—

How would it be to advertise for further copies of the pamphlet; for, if 500 were printed, others almost certainly exist somewhere, and the date of acquisition in some cases might be recorded or be otherwise ascertainable?

Such attempts have now been made.

Dr. Putnam very kindly advertised for a copy of the 1849 booklet, but without success, as explained in his letter of Feb. 13, 1914 :—

We advertised for Sleeper's "Shall we have Common Sense?" in the 'Bookseller, Newsdealer and Stationer,' and also in the 'Publishers' Weekly,' on November 10, 1913, but no reply of any sort has been received to the advertisements. Our failure to find by this means a copy of the edition of 500 copies supposed to have been issued 65 years ago would not appear *per se* to argue such an issue as improbable.

With regret at our inability to aid you further in this matter.

Mrs. Endicott also kindly advertised in November, 1913, for information concerning the pamphlet in the 'Boston Transscript,' and has recently drawn my attention to another advertisement to the same effect which appeared at the beginning of last March in the same paper. No reply was evoked by either of these.

6. *The Entries in G. W. Sleeper's Diary for* 1849.

The diary, kindly sent to me by Mr. J. F. Sleeper, was a little bound volume for the year 1849, so arranged that each of its pages held spaces for the entries on three days. The entries had been struck out, sometimes with pen, sometimes pencil, but were still legible. Under the date Thursday, April 26, was the entry "Copyright ·50," and under Friday, May 18, "Bense Pamphlets $30.00." If other details of the expenditure of a prosperous business man, as Sleeper was then, had been entered with equal care, the diary would have been far more crowded than as a matter of fact it was. The page including April 26 held no entry except the "Copyright," the opposite page held two entries; the page including May 18 held three entries in addition to the "Pamphlets," the opposite page two entries.

I was anxious to know if the fifty cents conformed to the law at the time, and also whether there was any entry in the record book for April 26, 1849, that might have escaped notice. I therefore wrote to Dr. Putnam, who very kindly sent me the following result of a renewed search made by the Register of Copyrights:—

From the Register of Copyrights,
Sept. 12, 1913.

To the Librarian of Congress,

Referring to the inquiry from Prof. E. B. Poulton.

Professor Poulton asks that the Copyright Office record book for the year 1849 be searched under the specific date April 26, for possible entry of Mr. Sleeper's book. We have done so, but find no registrations at all on April 26 of that year. As stated in my previous "Memorandum," we had already examined the record book page by page for the year 1849 without discovering any entry in regard to Mr. Sleeper's book.

He also asks, in view of a notation in Mr. Sleeper's Diary, what the legal copyright fee was at that date, and whether the copyright could have been registered before the book was published.

The answer is that any registration in 1849 must have taken place under the provisions of the Act of February 3, 1831, which provided in sec. 4 as follows (in part):—

> "That no person shall be entitled to the benefit of this Act, unless he shall, *before publication*, deposit a printed copy of the *title* of such book, or books, map, chart, musical composition, print, cut, or engraving, in the clerk's office of the district court of the district wherein the author or proprietor shall reside, and the clerk of such court is hereby directed and required to record the same thereof forthwith, in a book to be kept for that purpose . . . . For which record, the clerk shall be entitled to receive, from the person claiming such right as aforesaid, *fifty cents* . . . . And the author or proprietor of any such book, map, chart, musical composition, print, cut, or engraving, shall, within three months from the *publication* of said *book*, map, chart, musical composition, print, cut, or engraving, deliver or cause to be delivered a copy of the same to the clerk of said district. . . ."

Respectfully,
Thorvald Solberg,
Register of Copyrights.

It is therefore clear that the date and fee of the copyright are entered in accordance with the law existing at the time; although, in the absence of confirmation, they are valueless as evidence of the publication in 1849. Sir George Warner, in fact, considered that the diary does not support the genuineness of the pamphlet, for he wrote, Sept. 6, 1913:—

I am not satisfied with the entry in the Diary, 18 May, and instead of removing my suspicions it merely increases them. The ink in which it is written looks as if it had been doctored to give it the appearance of age, and neither this entry nor the others in which the same ink is used have quite the character of G. W. Sleeper's hand—they seem imitative rather than natural, *e. g.* compare "Burrill," 20 May, with "Burrill," 15 March, and the entry on 22 May with the other "Nash" entries. The object of more forged entries than one would of course be to make any peculiarity in the appearance of the entry less marked. On the other hand, assuming all the rest of the entries to have been Sleeper's, his hand certainly does vary to a certain extent, as everyone's does when writing at different times and under different conditions. So far therefore the evidence is inconclusive, and I am very glad to hear you are in communication with Bense's daughters. If his ledgers or business accounts are in their possession, they ought to settle the matter *; but it will be something, with regard to the contract, to get specimens of his signature and handwriting †. I am inclined to think that the 18 May entry and the contract were written by the same person, so far as I can remember the latter.

7. *Manuscript exhibiting Appearance of Artificial Treatment with a Brown Stain.*

Mr. J. F. Sleeper kindly sent to me, Aug. 10, 1913, a number of short manuscripts, probably the original rough drafts of a series of articles for the press entitled "Thoughts of an Atheist." Some of the pages were written on the backs of sheets dated 1851 and 1852, and accompanying them was a manuscript letter, protesting against slavery, signed "A Southerner," and dated Aug. 14, 1852. This, like the "Thoughts," was evidently intended for the press, and probably published. There seems little doubt that all were written within a few years of 1849, yet the contrast between them and the pamphlet is immense. The "Thoughts," which convey no suggestion of originality or power, include discourses on the following subjects:—(No. 7) On laws and their enforcement and on the atheist being compelled to give evidence on oath—although meaningless to him; (No. 8) On the atheist being as good as any other man; (No. 12) On the brain of animals and man, and on mind as the product of brain and therefore of matter; (No. 13) On animal sagacity and instinct; an unnumbered paper on the inconsistencies of the attributes of the Deity.

No. 9 was of interest in a very different way; for it had obviously been treated with a brown stain, apparently laid on by a brush or rubbed on by a broad surface, perhaps the end of a finger or a painter's stump.

Mr. J. F. Sleeper suggests that a fluid may have been spilt over the manuscript, or mildew formed in the creases, and that after some chemical had been then brushed over the surface in order to remove the effect, the iron in the ink had in time caused the stain. He has not seen such an appearance on any of the other papers.

This curious-looking document was submitted to Sir George Warner, who wrote Aug. 28, 1913:—"No. 9 has a very queer appearance. Is the stain tobacco-juice or what? It is obviously artificial and intentional, and not the natural discoloration of time like that on No. 8; but this again, I think, is not the same as that which is on the contract."

8. *The Paper of the Booklet dated* 1849.

The present section does not contribute evidence for or against the authenticity of the work; but it is desirable to render the enquiry as thorough as possible, and to throw further light on a subject already investigated up to a certain point.

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* See p. 31.

† See p. 32.

Mr. Lewis Evans and Mr. Johns expressed the opinion, at the time of last year's address (p. 40), that the paper is probably a Dutch hand-made.

The late Mr. De Vinne also informed me, Aug. 25, 1913, that "the hand-made paper sold in the United States about 1850 was largely of Dutch manufacture."

It is now possible to come to a definite conclusion concerning the watermark, which appears on pp. 19–20 of the booklet, and concerning the letters 1 V to be made out from pp. 9–10 and 25–26.

Last summer, Mr. Horace Hart, continuing the skilled help which he has always given me in this enquiry, sent a photograph of the watermark to Mr. C. H. Balston of W. and R. Balston, Ltd., Maidstone, proprietors of the Whatman paper. Mr. Balston recognised the device as that distinctive of his firm for paper of Royal size (19 in. × 24 in.), namely, a shield with three diagonal cross-wires. He furthermore stated that the form of the device was of an old type, shewn, by a fine series of samples kindly submitted by him, to have been altered by 1831, when a broader bolder pattern was substituted, and has been continued unchanged to the present day. Unfortunately the photograph sent to Mr. Balston did not include the lowest part of the device, which in the Whatman watermark terminates with a W, but in the pamphlet with a simple point, making a V. I wrote explaining this to Mr. Balston, who replied, Nov. 11, 1913:—

> If, as you say, the monogram in the watermark finishes off as a V, and not as a W, then I agree with you that the device is probably a pirated one. I noticed in your photograph the centre of the W did not appear, but as it was on the extreme edge of the print, I thought possibly that its non-appearance might be due to a fault in the printing, or that it appeared lower down, so I did not attach much importance to it. Another point which struck me was that the upright lines were not the regulation distance apart, namely 1$\frac{1}{16}$″, which is invariably the case in all the samples I have of this size from 1781 up to the present day. In the photograph showing the monogram they are 1″ apart. This might be due to shrinkage of your printing paper after washing the print, so I attached no importance to it. You could, however, verify this point by measuring the original. I have made a fairly extensive search through all the old papers and have been unable to find any watermarks with the characters 1 V, as referred to in your letter of July 14.

The letters I V are clearly to be explained as a fraudulent rendering of J. W. (for James Whatman), which appear on the earliest Whatman sheets, viz. 1781 and 1784 in the specimens sent by Mr. Balston. It is probable that the imitated paper was of very early date; for in 1808 and 1810 J. W. is replaced by J. Whatman, while W. Balston is added, although omitted from later years, viz. 1831 and 1834.

The upright lines of the pamphlet are not spaced at regular distances, some of them being 1 in. apart, others as much as 1$\frac{1}{8}$ in.

Considering the evidence as a whole, there can be little doubt that the paper of the pamphlet is of Dutch manufacture and that it bears a forged Whatman watermark of early date in the history of the firm. Having undertaken this enquiry I have been anxious to pursue it to the end in every detail, although fully aware that the identification of paper and watermark throws little light on the date of the pamphlet, for in the words of Mr. Lewis Evans:—

> Should anyone in America, say in the seventies, have contemplated a literary forgery purporting to belong to the forties, he might easily have got enough suitable paper for the purpose of printing a few copies, either from some old blank books or conceivably from some little lot in stock in a printer's warehouse . . . . Aug. 18, 1913.

9. *A Manuscript Lecture entitled "Life and the Cosmosite" as Evidence for the Booklet dated* 1849.

Mr. J. F. Sleeper has kindly permitted me to see the following letter addressed to his father:—

> Boston, Nov. 5/50.
>
> My Dear Sir,
>
> You are cordially invited to deliver your Lecture—Life and the Cosmosite at the meeting of the Society * next Monday.
>
> Ever &c.,
>
> James W. Stone †.
>
> Mr. Sleeper.

Accompanying the letter was a manuscript of rather closely written pages ($8\frac{3}{8} \times 6\frac{3}{8}$ in.), bearing the title "Life and the Cosmosite," and purporting to be the lecture of Nov. 11, 1850, delivered in response to Dr. Stone's invitation. The lecturer speaks of being "about to address you this evening at the liberal invitation of Dr. Stone . . . ." He continues, after a brief introduction, "In 1847—only three years ago in this very city—some of you will doubtless remember I delivered several Lectures, one on the Origin of Life and the Advance of Civilization, ..." He then goes on to speak of their hostile reception, concluding this part of his lecture in the following words:—"These good Christians, ... were also zealous to show their pious faith, by publicly burning my 'blasphemous pamphlet,' that is, the few that they could lay hands upon . . . . All this tempest rose because a man who had thought and experimented and reasoned and reflected tried to place before his fellow-men the results he had theoretically and experimentally arrived at" . . . . "It is this theme (with your kind permission) which I intend to review to-night, and in doing so I hope to reveal my thoughts in a somewhat clearer manner—." The lecture proper then opens with a paragraph beginning—"As I then was at pains to try to prove" and continuing with the substance—often word for word the same—of the second and third paragraphs on p. 3 (p. 3 of the present Appendix) of the 1849 pamphlet. The last three lines "may be greatly modified . . . . its kind" on p. 3 appear word for word on a later page of the lecture. The passage referring to the triad of Lemur, Monkey, and Man (Appendix p. 5) also appears in nearly the same words. The two sequences of stages (Appendix p. 8) are also given—fused together and almost complete. The lecture concludes, as does the 1849 pamphlet, in argument directed against the existence of a Personal Deity. As evidence there is brought forward the "fact . . . . . that the air, &c., is filled with myriads of deadly germs." Apart from the above, the lecture is almost entirely devoted to the contention that the germ of every animal and plant has always existed and will continue to exist for all time, that it may lie dormant for long periods until called into activity by favourable circumstances which determine the particular form its reincarnation will assume. All germs are apparently to be traced back to an electrical primal germ containing "within it all the essentials of all Life that it is possible to create—Cosmosite . . . . or 'germ-world-inhabitant.'"

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* The Massachusetts Medical Society is the only one which Mr. H. G. Wadlin, Librarian of the Public Library of the City of Boston, can suggest. He kindly wrote, Feb. 12, 1914:—"A search of the Boston newspapers of Monday, November 11, 1850, and previous and subsequent dates, revealed no notice of the lecture by G. W. Sleeper.

"No mention of the lecture before the Massachusetts Medical Society is found in 'An Index of Medical Communications, Library of Practical Medicine, and Publications of the Massachusetts Medical Society, 1790–1901. Prepared by the Recording Secretary. Boston, Clapp, 1903, 40 pp., 8°.'"

G. W. Sleeper's lecture would hardly fall into the category of "Medical Communications," so that the absence of a record is probably unimportant.

† The following information has been very kindly sent to me, Feb. 12, 1914, by Mr. Horace G. Wadlin;—

The 1850 Boston Directory gives the address of Dr. J. W. Stone as 6 Bowdoin Square, h. do.. "The Harvard Medical School, a History &c. by Thomas F. Harrington," Vol. 3, p. 480, No. 794, has the following record of Dr. Stone:—

"James Winchell Stone, A.B. 1843; A. M.; b. Oct. 26, 1824, Boston; d. Aug. 20, 1863, Dorchester. Practiced Boston. Collector Internal Revenue, 3d. Massachusetts District. M. M. S. S." From 1857–1862 Dr. Stone's residency was Cottage Street, Dorchester.

"Harvard College, Class of 1843, Memorabilia, 1883, Prepared by Wm. A. Richardson," has the following entry relating to Dr. Stone:—

"James W. Stone, Boston (Roxbury, Mass.), Descendants, Ella G. Stone Florence, Italy; Frances Tyler Stone, Florence, Italy."

It will be realized from the above account that the lecture itself is of no great interest or importance, except as supplying evidence that the booklet dated 1849 is genuine. The validity of this evidence again rests upon the authenticity of Dr. Stone's invitation. Accompanying the latter were three other documents signed by J. W. Stone. One of these dated Aug. 11, 1856, introduced "my friend George W. Sleeper, Esq." to the Hon. R. G. Hazard. A second of the same date, written to G. W. Sleeper, suggested that the same introduction might be shown to others, who are named. The object in view was probably political, viz., "doing something for the good cause of Frémont and Dayton."

A third document, dated Boston, May 23, 1854, certifies that Dr. Stone had known "George W. Sleeper for some years as an active, determined, paying, and working member of the Suffolk Free Democratic Ward & Co. Convention, of which he was one year the Secretary."

There was something in the handwriting of the invitation, when compared with that of the three other documents, which roused my suspicions. I sent all four to Sir George Warner and asked for his opinion. He kindly replied as follows, April 18, 1914:—

> I return the four additional letters which you have sent me. I am unhesitatingly of opinion that the one dated 5 Nov., 50, is spurious. It is almost enough to place the four letters side by side, when the difference of its handwriting from that of the others is at once apparent. Instead of being easy and natural, it is laboured, halting, and plainly imitative. But there is other damning evidence. The paper (*a*) is the same make as that of the letter dated 23 May, 54 (*b*), and is, I have no doubt, the originally blank second leaf of the same sheet. You will see that the left edge of *b* is slightly rough, showing that it has been cut with a paper-knife. If you lay *a* upon *b*, making the right edges exactly even, you will find that the width is not quite the same, and that the left edge of *a* has been trimmed (so as to avoid a suspicious rough edge), but not quite straightly. It has also been carefully torn, evidently with design, so as not to show the same holes as are in *b*, and also for the purpose of destroying the evidence of the date in the endorsement. Nevertheless, by laying the one leaf carefully over the other, as I have said, the top hole and the next will be seen to fit in exactly. This would hardly be the case unless *a* and *b* were the two leaves of the same sheet, any more than the original folds would exactly coincide, as in fact they do.

The folds spoken of by Sir George Warner traverse the leaves in both directions—three across and two longitudinally—so that the case against coincidence is much stronger than it would be with the two leaves of most letters. The four holes are perforations by which the letter had been doubtless attached to others in pamphlet-like form, and a part of the circumference of the third hole as well as that of the first and second is still visible, in spite of the torn edge. The only one that has been entirely removed is the fourth and lowest. Examination with a lens shows that the portions of the three upper holes resemble the corresponding parts of the entire holes in their darkened colour as well as their precise form. The endorsement has not been wholly torn away. "Dr." and "18," the first two figures of the year, were no doubt intentionally left. The blank sheet was probably damped and ironed in order to alter its appearance as far as possible.

Sir George Warner's convincing proofs that the invitation was forged are, of course, sufficient evidence that the manuscript lecture, which opens with a reference to the invitation, is also fraudulent.

10. *The Use of the Word "Agnostic."*

Mr. J. F. Sleeper wrote May 10, 1913, stating that the word Agnostic was invented by his father in 1846 and that he used it in several lectures. The manuscript of the lecture in which the word was introduced was the first of all documentary evidence submitted to me. The lecture is entitled "*On Our right to express our Ideas and the value to Mankind of that expression.*"

Speaking of "men who dared to *think* differently from their less-educated or less-original fellows," and who, although persecuted in their own age, were honoured in later generations, the manuscript continues:—

> These men I shall designate as "Agnostics"—as differing from the mere Atheist, under this term I comprehend much: I mean it to signify a man of advanced ideas who confesses he has *not* attained perfect worldly wisdom, who admits he does not know all about "God" and "a future state," who is an honest asserter of ignorance on all matters not proven to him by actual Scientific demonstration, and to whose reflective mind the mere verdict of a majority carries little weight. Which, as you will see, is precisely the reverse of the word "*Gnosis*" and of the professions of the old Gnostics (as described by the Rev. Taylor in his Diegesis on page 37)—in several respects—and is also in defiance of those bigoted, all-knowing, persecuting and pitiless imparters of divine revelation whom I would call Torarians from the Hebrew word *Torah**.

The manuscript is signed with the initials "G. W. S.," and is undated. Mr. J. F. Sleeper informs me that his father said the lecture was delivered during the latter part of 1846. The date can be inferred by means of a quotation from the "poet Mackay," who is said to have "just composed the lines—

" . . . . . We wonder long
That hate had power to lead our fathers wrong
Or that false glory lured their hearts astray
And made it virtuous and sublime to slay."

Mr. J. F. Sleeper tells me that these lines form part of a work entitled 'Railways' dated 1846.

The circumstances under which Huxley introduced the word "Agnostic" in 1869 were quoted in last year's Address (pp. 44–5). Although no comparison is possible between the literary form of the two accounts, the line of thought is precisely the same, and adds another to the long series of improbable coincidences involved by the hypothesis that the booklet is genuine. But the facts proved in sections 2, 4, and 9 show that it is not genuine, and we are driven to conclude that the manuscript is a late fabrication, and that the manner in which the date is revealed without being stated, as well as the addition of "Torarian" are parts of an elaborate scheme intended to throw the critic off his guard. It was probably foreseen that there would be a tendency to argue thus: "The date is so important that a forger would certainly have added it: therefore, as it has not been added, the document is genuine."

11. *The* 1860 *Pamphlet is inconsistent with the Booklet dated* 1849.

It was pointed out on p. 43 of last year's Address that the comparison between the two pamphlets was unfavourable to the authenticity of the one with the earlier date. A further serious inconsistency was pointed out to me by Mr. Howard M. Chapin, Librarian of the Rhode Island Historical Society, Providence, and was afterwards independently observed by my friend Professor Lotsy, of Haarlem. The Introduction of the later pamphlet opens with the words

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* Signifying inspired teaching.

> This lecture is founded upon a theory, entirely original upon this side of the Atlantic, and which first developed itself in my mind about the year 1853—at which time I published a small article in a Boston paper, from which nucleus was produced and delivered the greater part of this discourse, in the year 1856, before the Hopkins Literary Association. of North Providence—of which I was then President—in which capacity, I became acquainted with F. W. Miner, who, to reciprocate a like act, invited me to deliver it before the South Providence Lyceum, where it was also well received.
>
> The next delivery of it occurred from an invitation to present it as the first, or opening lecture of the "Member's Course of Franklin Lyceum Lectures," which was done, and it stands so recorded—notwithstanding every means have been used to efface it.

The Introduction then goes on to speak of the attempts made to deliver the lecture on Feb. 8 and again on Feb. 24, 1860.

I have quoted the above sentences in order to shew that the author was extremely careful to give the history of the development and the exposition of his thoughts on education in relation to civilization. And yet these very thoughts are set forth in considerable detail on pages 12–18 (also 12–18 of the Appendix to the present Address) of the 1849 booklet, stated in the Introduction to contain lectures delivered in 1847, and to be founded on ideas which entered the author's mind when he was 17, viz., in the year 1843. We cannot doubt that if the pamphlet dated 1849 had been in existence in 1860, the author would have referred to it in his Introduction.

Mr. J. F. Sleeper maintains, on the contrary, that there is a real difference between the two pamphlets, which accounts for the want of any reference from the later to the earlier. He states that in 1847 his father looked upon Education as the offspring of Civilization, but in the next decade regarded Civilization as the offspring of Education. I am sure, however, that no one can read pages 12–18 of the accompanying Appendix without recognising the fact that Education is given the primary place, just as in the 1860 pamphlet, and that "the advance of civilization" spoken of in the title (Appendix, p. 1) was a progress which the author maintained in that very lecture to have been brought about by "Mother Education" (Appendix, p. 17).

12. *The Booklet contains Ideas implying Knowledge much later than* 1849.

My friend Professor Van Bemmelen, of Gröningen, has pointed out to me that the ideas on the germinal origin and germinal transmission of characters set forth on pp. 10, 11, and 14 (also pp. 10, 11, 14 of the Appendix) of the 1849 booklet, and quoted in last year's Address (p. 31), imply a standpoint of knowledge and hypothesis that is much later than 1849. The passages referred to pre-suppose the equality in heredity of the germ-cells of the two sexes. Yet this conclusion is only implied and not announced as the important new thought it would have been in 1849. The same criticism applies to the work as a whole, which, apart from the discoveries announced in it, seems to belong to the intellectual atmosphere of a far later date.

My friend Professor August Weismann tells me that the conclusion that the male and female germ-cells are essentially similar, and play the same part in heredity, was first published in his memoir "Beiträge zur Naturgeschichte der Daphnoiden," Leipzig, 1876–79, p. 323.

13. *The "1849" Booklet probably of very recent Date.*

In May 1913 I had no reason to doubt the history of the copy given on pp. 26–27 of last year's Address, and considered on p. 43 to be the strongest evidence in favour of authenticity. The facts that have now been proved make it impossible to accept this history without further confirmation, and as yet such confirmation is wanting.

The attempt was made to trace the book-store at Cleveland or Cincinnati where Mr. Miller stated that he had bought the booklet (pp. 26–27). A letter directed to "Mr. W. Davie, Book Store, Cleveland," was returned with the stamp "Not in Directory No. 8." A similar letter directed to Cincinnati was not returned, but brought no reply, and a second letter to the same address was equally unsuccessful. My friend Dr. Joseph L. Hancock, of Chicago, has been unable to find evidence in the Directories that anyone named W. Davie is now keeping a book-store in either city.

The attempt to obtain confirmation has therefore failed, and we cannot accept the history of the copy sent to Dr. Wallace. If the booklet is a forgery, as there is the strongest evidence to prove, it is only reasonable to suppose that it was printed after *all* the discoveries announced in it had become known, and perhaps after the death of G. W. Sleeper in 1903. This suggestion was made by Sir George Warner in a letter dated Aug. 17, 1913:—

> The possibility of a fraudulent concoction after G. W. Sleeper's death had occurred to me. If, however, Miller's statement that he purchased his copy of the pamphlet in 1892 is correct, this cannot be, and the fact that the pamphlet is mentioned * in the obituary notice of 1903 is also against it. . . . But, on the assumption that the date 1849 is genuine, the wonder to me is that the author apparently does not refer to the theories advocated in this pamphlet anywhere else among his later publications, and that no claim to anticipation has been made on his behalf until now, although he lived to so

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* This is a mistake (see p. 43).

late as 1903, and his son shares his views and seems fully alive to his pre-eminent merits . . . . . . I am still rather sceptical, and look forward with interest to the arrival of the Diary, which ought to settle the matter as you say . . . . .

As a matter of fact, the pamphlet dated 1849 is *not* directly mentioned in the obituary notice of 1903.

When the account of G. W. Sleeper in the 'The Truth Seeker' for October, 1903, is carefully compared with the further references to him in the obituary notice of his wife in the same journal, for January 13, 1912, certain differences are apparent.

The earlier notice speaks of his "little book, entitled 'Education and its Offspring—Civilization,'" of "various ideas put forth in his numerous essays and speeches," and states "he was the first to advance the theory that germs cause most diseases, and further maintained that life was due to other organisms diffused throughout the atmosphere, requiring only favorable conditions for its development. Numerous novel thoughts concerning civilization likewise emanated from his mind, ..."

There is no reference to the 1849 booklet, and the words I have quoted give a very imperfect idea of its power and scope. And yet a sentence in the notice, quoted as one of G. W. Sleeper's "oft-repeated utterances," appears almost word for word * in the pamphlet, viz., the sentence beginning "Of what lies beyond the grave" and ending "need not fear to die" near the top of p. 17 (also p. 17 of the Appendix to this Address).

The references in the obituary notice of 1912 are very different. "The Origin of Life" and "The Dangers of the Unseen" are spoken of as lectures published in 1849, while the main subjects of both are set forth in brief but adequate summaries.

The above comparison strongly suggests that the 1849 booklet was printed after G. W. Sleeper's death. The printer's signature to the contract taken alone is probable evidence for thirty or forty years after 1849. The special mention of the house-fly as a carrier of disease is evidence for a much wider interval.

I have carefully read more than once everything in print and everything in manuscript by G. W. Sleeper that has been sent to me by his son, and I fail to see any evidence of that ability which would certainly be required to produce the booklet if it were written to-day. The evidence of ability is probably chiefly displayed in fitting the accounts of modern discovery into the framework of an older phraseology. The conclusions of modern science may well have been derived, as Sir George Warner suggests, from a *résumé* of recent discoveries in some scientific publication or magazine.

On the other hand, the fact that G. W. Sleeper is described as a printer (p. 28), and that some of his manuscript shows the signs of artificial treatment (p. 35) are in favour of the conclusion that the fraud was perpetrated by him.

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* The only verbal differences are the substitution of "can" in the notice for "may" in the booklet, and of "all his fellow-men" in the former for "all" in the latter. There are also slight differences in punctuation, capital letters, &c.

14. *The probable Motive of the Forgery.*

The consideration of motive seems to be almost a waste of time, but so many friends have raised the question "Why should anyone have done such a thing?" that I think it may be interesting to attempt a brief discussion. The most probable explanation is, I think, as follows:—

G. W. Sleeper was a man who loved to lecture and to take every opportunity of publicly expressing his views. He was probably far more wounded by ridicule and neglect than by any violent attack. The following reminiscence by an old resident of Providence was kindly sent to me by Dr. Putnam:—

> I knew George W. Sleeper by sight, but was not acquainted with him. He kept a tea store as stated. He advertised a lecture about the year 1860, the subject being 'Education and its Offspring, Civilization.' He may have put this in pamphlet form, but I do not remember of seeing it. There was a tendency to ridicule his literary aspirations and he was hardly taken seriously. Excepting in that early time I do not remember of ever hearing of him, and I do not know that he remained in Providence.

Sleeper's intense belief in himself would only have been strengthened by opposition, and still more by his failure to command serious attention. He probably quite honestly believed that the vague ideas which occurred to him were of momentous importance in the history of science, and that when he had put the results of his reading in his own words he was announcing original discoveries. Then, as the years went by, such ideas as natural selection, the origin of man, the continuity of the germ-plasm, the germ-theory of disease, resistance, the mosquito and the house-fly as carriers, sprang into existence and instantly became centres of intense interest. In each of these successive discoveries and many others, Sleeper's self-centred egotism would recognize the natural outcome of thoughts received so very differently or not received at all when he had spoken them. One thus self-deceived as to the importance of his own ideas would certainly honestly believe that he had been, and was still, the victim of bitter injustice, and he might defend the falsification of evidence on the ground that only in this way could justice be done not only to himself, but to the history of thought. He would argue "All these vaunted discoveries are the simple and easy development of original thoughts which I announced half a century ago, and it is only fair and right that they should bear the date of their conception as well as that of their birth."

The above attempt to analyse the psychological situation assumes that the forgeries were committed by G. W. Sleeper himself; but the same explanation may be offered if we suppose that they were committed by another who knew his feelings and shared his delusion that he was the victim of injustice.

APPENDIX.

A Reprint of the Booklet by G. W. Sleeper, dated 1849, and forming the Subject of the Presidential Addresses in 1913 and 1914.

The work has been printed as in the original, page for page and line for line, and the type has been matched as nearly as possible.

All the mistakes of the original have been preserved, with the exception of a few letters or hyphens which have slipped at beginning and end of lines. These instances are noted below :—

Page 1, l. 5.	all- (*raised hyphen*).
,, 3, l. 15.	infinitesimally (*raised* i *at beginning*).
,, 3, l. 24.	characteristics (c *lower down*).
,, 4, l. 4.	conception, (*comma lower down*).
,, 5, l. 11.	il (*slight space between* i l).
,, 5, l. 27.	species, (*raised comma*).
,, 8, l. 11.	in (i *lower down*).
,, 8, l. 15.	germ, (*raised comma*).
,, 11, l. 6.	dis- (*raised hyphen*).
,, 12, l. 15.	un- (*raised hyphen*).
,, 15, ll. 3, 4.	ing . . . ly (i *and* l *lower down*).
,, 15, l. 9.	ignorant (i *lower down*).
,, 16, l. 18.	ish (*raised* i).
,, 19, ll. 1, 2.	not . . . the (t *and* e *lower down*).
,, 23, l. 1.	re- (*raised hyphen*).
,, 24, l. 27.	hu- (*raised hyphen*).
,, 25, l. 26.	ier (i *lower down and slight space between* i *and* er).
,, 27, l. 12.	fi- (*raised hyphen*).
,, 29, l. 13.	having (*slihgt space between* n g).
,, 31, l. 4.	men- (*raised hyphen*).
,, 36, l. 5.	cre- (*raised hyphen*).

SHALL WE HAVE COMMON SENSE

SOME

RECENT LECTURES

WRITTEN AND DELIVERED BY

GEO. W. SLEEPER.

BOSTON:
WM. BENSE, PRINTER.
1849.

Entered according to Act of Congress, in the year 1849, By GEO. W. SLEEPER, in the Clerk's office of the District Court of Massachusetts.

INTRODUCTION.

The original ideas on which these lectures were founded, entered my mind when I was barely seventeen, and during their gradual development the major portion of both of the lectures were committed to paper in the course of the past six years. The first public delivery of either occurred in Boston about two years ago, it was, however, almost impossible to obtain a hearing for them so bitterly hostile did the audiences (assemblies little better than savages) prove themselves to be, and so persistently did they interrupt, and endeavor to overawe, the lecturer.

Such being the condition of society, and as the press of this city, influenced by certain clergymen, have not seen fit to acquaint the public either with the substance of the ideas set forth or with the facts relating to the attempts to deliver the lectures containing them, I decided to put these subjects to print; as being the only way open to secure attention from the many fair and noble minds among our citizens who undoubtedly have Common Sense.

THE ORIGIN OF LIFE

AND THE ADVANCE OF CIVILIZATION.

Let us take a cursory survey of an abstruse subject, one that has naturally woven an ever-fascinating, a mind-stimulating and an all-powerful spell over the vast majority of the deep thinkers of past and present ages.

Born out of the womb of Night; dwelling in the house of Night; and fading away in the embrace of Night—how mysterious, how difficult, how remote is this interesting phenomenon: The Origin of Life, on which scientific and speculative Man vainly ruminates and theorizes while borne dreamily along on a hastening current of hopeless perplexity and confusing course; and yet on which a so-called God-inspired Bible assumes to expound with authority and to relate with truth!

In this legend Man and all the Animals are introduced as creations of a single day! Geology has dispelled that illusion from minds open to admit the irradiating light of Knowl edge. And it is also fabled that all this work of Creation occurred but six thousand years ago! Which Creation, the state of civilization in India and China some five thousand years back, is sufficient to disprove without the abundant aid derived from Geological evidence; all proving an inconceivably ancient history for Man.

Leaving the crude, brief, unsatisfactory and incredible account of the Creation given in Genesis to its inevitable and unregrettable fate, as one of the most audacious insults ever offered to the human intellect; a reasoner is irresistibly drawn on to conclude that Man has been impelled, as Education gradually expanded his growing intellect and drew him away from the evil grasp of the deceiving priest in the dense shadow of the enslaving church, to read with more and more deductive attention the open book of ingenuous Nature under the blue dome of a clear sky in the frank light of day.

Thus has he been broadeningly led to inspect the vastly altering geological strata, to compare the multi vegetal transformations occurring from age to age, to meditate upon the remarkable fossils re-constructed by the amazing genius of Cuvier, to study the involved appearances, disappearances and relations of long bygone or of still living races of barbarous and civilized mankind and also of species, varieties and individuals of animals, plants and minerals in their likewise complex inter-relations, differences and ramnifications: aye, until even like Baer he discovers the true seat of the human germ of Life.

As a grandly final result of his readings, his reflections, his searches and his experiments he finds that Life owes its faint beginning to primal germs. These germs I hold to be infinitesimally minute living atoms pervading the entire terrestrial atmosphere; and, perhaps, the entity of the Cosmos.

Perishable themselves, each is the common carrier of the principle of Life which is indestructible and eternal, and each is lastingly imbued with the peculiar characteristics of the species and, but less so, of the individual its particnlar variety alone is able to form. The characteristics and attributes of any germ may be greatly modified or limitedly altered during its union with its sexual opposite to form its kind, Arranging themselves in strict obedience to dominant Natural laws of which we have but little knowledge, in a vastness of Space of which we have no intelligent conception, and exhibiting an almost unmeasurable minuteness reducing our feeble powers of comprehension to appalled nothingness, these germs are slowly developed, altered and perfected during an immensity of periods of time compared to which the six thousand years of the Bible is but a trifling era—a pebble on the sea shore; a tiny star in the Milky Way.

These germs of life and the individuals growing out of them, were constantly experiencing change. Weakened by exposure and attack they were only preserved unmodified for a brief (though variable) period by means of the more or less effectual resistance they were able to offer to climatic conditions, changes of food, convulsions and transformations of Nature and the destructive inroads of overpoweringly hostile forms of reptile, piscine or animal Life For example: just as most of you have beheld a neglected flower perishing in the midst of over-topping weeds or languishing for lack of the vital sustenance that grass or clover has withdrawn from its starving roots

How these tiny germs first creatively grouped together, at Nature's will, out of the vast chaotic void; what the first formed creature was and what amazingly prevailing law compelled their more passive obedience to its mute behest than ever the humblest of the nations abjectly rendered unto the loudest mouthed decree of imperial Alexander; will probably remain forever enshrouded in clewless mystery darkly closed as the burned tomes of the Sybil to the anxious inquiries of investigating Man. I should venture to imagine, taking the researches of Leeuwenhoek, of Swammerdam and of Schwann in consideration together with the results I have tediously arrived at by microscopical and generative experiments, that germ cells of the simplest form at first existed; that these obeying the Unknown Cause I have alluded to, gradually extended themselves branching out like the Banyan tree, but to generate, or metamorphose into, more or less progressive species or varieties; the lowest the next higher, and so on, trilobite to mammal: one of the many branches necessarily terminating temporarily in a triad: the Lemurs, the Monkeys, and—Man himself.

Thus appeared the original of our species, not fashioned out of clay or after God's image; originally naked, savage ravenous, lustful, unsympathetic and revengeful, he has never retrograded, but at all times in one portion of the world or another has steadily advanced, raising himself ethically and intellectually throughout the course of the ages entirely without the aid of supernatural revelation or divine assistance, simply by his own increasing Reason and that Experience which so admirably cultures the tender flowers of Morality while eradicating the hardy weeds of Vice; and also by his own persistent efforts stimulated by Education,—but always, though more or less hairy and uncouth, he was, nevertheless, essentially Man.

And as such he cannot but remain.

I am well aware, Ladies and Gentlemen, when I make the broad statement that Man and the Ape are co-descended from some primary type, that there is little resemblance in face or figure between the nude forms of the symmetrical, pleasing, beautiful Apollo and Venus that the surpassing art of Apelles and Praxiteles has richly bequeathed to us and the ungainly, loathly and ugly contour of the Simian tribes; but remember that it is not to the higher evolutions of Man nor to the lower variations of the Monkey that we must look in this matter, but to just the reverse of each. And then in many respects a striking parallel is observed to exist between the "lord of creation" and his Quadrumana relatives the Chimpanzee and the Ourang Otang which clearly establishes the extremely rational view I have advanced and enables us to experience very little difficulty in tracing back these kindred creatures to a remote, an ancient, but a general stock; although exactly what that common forefather was is as likely to forever remain as profound a mystery as the astounding problem of how the beginning of things could take place or the absolute ending of all matter can ever occur!

We have never found any living or fossil link to form a chain between Man and the Ape, nothing to close the gap separating the two related animals like Owen's rhynchosaurus bonds the avines to the saurians, and the pliosaurus unites the pterodactyle to the crocodile. I doubt that any such creature will be discovered; to my mind there never was occasion for its existence: more likely some relic of an, at present, unknown animal proving to be the forerunner of both species, will be exhumed out of the debris of an age immediately antecedent to both: just as the gigantic mammoth was dug out of the congealing bosom of Siberia's ice in 1800 and the three-toed palæotherium, rude ancestor of our valued horse, was disinterred from the profound of the Eocene in earlier years.

The wonderful progressive presentation of forms ascending from day to day in the scale of organized beings exhibited by our species in the fœtal state and remarked by the physiologist, is another substantiation of my theory

Man, in the womb, passes through all the embryo forms of the types of the known divisions of animated Nature: first but a germ, he then resembles mollusk, fish, reptile, bird, rodent, ruminant, and batrich, finally assuming unmistakeable features of the human animal. Thus we see a significant panorama of the momentous changes which occurred in the course of ages displayed in the short space of nine months in the mysterious womb.

Primal matter to zoophyte, to crustacean, to fish, to saurian, to mammal and to Man! the inferior forms disappearing when their allotted work was done and the improved era no longer warranted theirthen inutile existence just as the platysoma of the Old Red Sandstone vanished in the Magnesian Limestone; or else becoming dwarfingly modified previous to extinction: similarly to the diminution of the seventy foot iguanodon into the four foot and perishing iguana which has outlived the age and environment which called its giant ancestor into being.

In this ever recurring disappearance, or modification, of animal and vegetable forms there is nothing strange. Everywhere about us we see waged the pitiless battle for life of which it is the inevitable outcome. Just as the dandelion, the plantain and the burdock extend their broad leaves o'er the verdure of the meadow, starving and exhausting the grasses around them; just as the weeds of the garden o'erwhelm with rank luxuriance the feebler cultivated vegetables during a brief period of neglect; and just as species of birds and animals become extinct from their merciless slaughter by barbarous man who spares not his own weaker kind, varieties of his race thus fading from sight; so there is a continual process of elimination and substitution going on in the great laboratories of Nature; the useless perish, the useful live and improve, although our conception of what is useful and improving is often opposed to Nature's.

All Geology indicates assured progress by its presentation of higher and higher generations of exalting forms, each remarkably suited to the peculiar age in which it appeared at its best. Of all such forms, that of Man would seem to be the masterpiece of Nature on this globe, and we cannot fail to be impressed by a conviction that whatever Nature may have accomplished on other planets, all her energies upon this have evidently been exerted, through the medium of Education, to shape, to instruct and to perfect, the Human Race.

But our parallel of comparison of Man with the Simians is effectually arrested by a three fold, irremovable, barrier: the possession of progressive, deductive and inventive Reason; the acquirement of extensible and transmissible Speech; and the innate knowledge of the formation and use of Tools; attributes resident solely in the spermatozoa and ovum of the human species, and absolutely inseparable therefrom. So I am spared the unpleasantness of announcing anything so distasteful, to you, as that the monkey was parent or progeny of Man; thus, this Scylla and Charybdis being happily steered past, I merely find it necessary to re-affirm my fixed belief in the gradual origination of both from a general parent, each distinct from birth and each preserving that distinctiveness unto the present epoch, modified somewhat, it is true, in the instance of the human individual owing to his germ-endowment with the rudiments of primarily cultivatible and incalculably higher functions.

I feel assured that skeletons or rock-preserved hairy specimens of this ancestor of the two species will ultimately be excavated from the strata preceding that in which remains of Man and of the Monkey have been found, to at once and forever confound the silly, the incredible, the sense-offending relation of the Book of Genesis; hashed together and served up to the simple by posturing and imposturing knaves of priests. The greater perishability and much more restricted production and dis tribution of the human frame in those remote ages, together with the very limited extent of the exploration of this but recently thrown open field have so far precluded success.

Thus, then, was Satyr Man. Behold him!

Education took this beastial, crude and ignorant Frankenstein horror by the clumsy hand and kindly began to lead him on in ever-gaining pursuit of the lofty ideal which alas we yet see flitting before us in the brightening distance, illusive, fanciful, unattainable, will 'o the wisp like, still. But nevertheless no chimera, like poor Ponce de Leon's Fountain of Youth, but a glorious reality, a luminous to-be of the glad time to come.

And her kindly care, Mentoring a Telemachus, which began with Man's stormy advent on this troubling planet; has never ceased, but has multiplied and multiplied, solicitously training the uncouth fingers of the undocile creature first to difficultly shape the roughly-sharpened knife of wood; next to fash ion the weapon out of fractured bone or shell; then to discard these for laboriously ground flint or stone; giving place, in turn, to more durable bronze or copper and yet again to the keener and harder iron or the tempered steel; improving the quality, increasing the number and extending the usefulness of her pupil's weapons and tools. Enabling the civilizing savage to exchange the damp, smoke filled, gloomy, bone strewn cavern for the dry, ventilated, cleanly mansion of wood, brick or stone elevating him to lofty distaste for the red fields of fiendish fray and sickening slaughter, the grim cannibal feast of flesh and blood and the disgusting orgies of sexual obscenity and drunken madness that characterized his earlier ages—insensibly drawing him slowly on to display kindness, sympathy and toleration towards his Brother Man.

Yes! Education, benificent Power, thou hast produced all of the "Material" whereof we of the earth have cause to be thankful for. And thou wilt produce incrdeibly more than even the most sanguine of us can venture to predict; besides incalculably ministering towards the true "Spiritual" of Man—not the ghostly, the priestly, the false intangibility of which knaves or fools so glibly presume to prate. For I disbelieve that in the marvellously complex piece of mechanism which we call Man (moved by some unknown Force pervading the Universe of which force electricity and chemical action are but a few of the observable effects) resides anything more "Spiritual" than can emanate from this Force: a Force which is manifested in the working of our brains and in the involuntary movements of our bodies.

Spiritualism plays no part in the great drama of this our life. Indeed, the sole phenomenon approaching to such is the departure of the life-germ from a perishing frame but to begin anew in another or an allied form. For nothing is lost in the vast economy of Nature: all things suffer but a transient change of form: thus the life germ resident in Man transmitted to his descendants, goes on existing indefinitely throughout all Time's infinitude of years; just as his Thoughts, those Genii children of his prolific brain, continue to live on ages and ages after that transitory organ has mouldered away into the dust of the long ago; and thus, and only thus, is Man immortal: in the transmission of his germ life and in the eternal perpetuation of his Original Thought.

Ladies and Gentlemen, pray excuse this long digression; I now return to my subject: I was remarking how Education had abated the savage and revolting appetites of Man, how she has fanned the flickering flames of melting mercy and soothing sympathy and sincere Brotherly love—qualities almost wholly wanting in the eldest of Earth's peoples—how she has dimmed the furious fire in the persecuting eyes of the religious bigot; quenched the fierce flare of his flesh consuming faggots and rusted for aye the levers of his muscle-rending racks; how it has raised the poor, the lowly and the ignorant and brought the rich, the high born and the learned down to a more common and less caste marked plane.

It has also insensibly, yet surely, softened the rigor of a host of heart breaking evils that ignorant men bore patiently, apathetically or helplessly in the long, dark, dreary times agone, simply because they knew no better, or adventured to breathe no murmur, or dared not rub the talismanic ring of Change—until Education with her Muses of Poetry and Prose; her Commerce and Travel; her Printing Press and Schools; her Gunpowder and her Agnostic with his untrammelled Thought, pointed out to them the very place to set the chisel of Emancipation upon the formidable gyves of venerable Tyrant Custom and ancient High Priest Superstition, and told them when to drive the keen edge through a rusty link with the Thor hammer of Progress wielded by the lusty arms of the Thinker of Free Thought. Alas! that even in this, the freest and fairest of all the countries on the Globe, the needed work should as yet have been so partially and haltingly performed: The taint of Slavery still adheres to us with rank repulsiveness and sinful shame. Abolished by England, France and Holland it is left for the land of freemen to stand shoulder to shoulder with Turkey and Muscovy in the rear ranks of Civilization's columns; its heel on the breast of the hapless Negro precisely as Muscovy grinds hers on the bosom of the cringing Serf.

Education, that must set both free, has yet to accord to us that Freedom of Speech, that Equality before the Law, now wrongfully denied to the poorer and weaker and the irreligious of the citizens of the World.

And to abate the lengthy hours of toil, the saddenning overwork of unjustly kept down women and stunted little children. And banish the brutishness of the majority of the people, the arrogance and frivolity of that minority: the rich and great, and the frenzying influence of the Arch Fiend, Rum. Above all it must exorcise the horrible nightmare Religion from every priest cursed land; substituting the pure, the noble, the holy creed of Thomas Paine: the Doing of Good to all in that common World which is our universal country. Thus shall we answer the problem of the wherefore of our existence as far as we can elucidate it; and thus reconcile ourselves to its certain termination, Death. Of what lies beyond the grave we know nothing—Death is a mystery we may never hope to solve; But he, whatever his race or creed, who tries to do right to all, need not fear to die.

Education has yet to remedy a multitude of evils besides those I have touched upon—civil, social, sexual and political; which cannot be entered into in the compass of this lecture. And she will do all this and more in the years to come; years which for her are eternal.

A great assistant to Mother Education in the tedious licking into shape of her bear-cub Man will prove to be the dawning but pregnant Science which the peculiar physiognomy of a schoolboy awakened into perception in the brilliant mind of the sage Spurzheim, later to be developed by the reflective Gall.

I allude to Phrenology, which young as I am, I have studied for the past six or seven years. I know it is a science at present held up to ridicule by the superficial, the unthinking and the ignorant; it is one, however, certain to become one of the most potent instructors of the race—one of the most tried and trusty staves Man has to lean upon for guidance and support. I cannot here enlarge on this miscalled "science of bumps" so despicably attacked by the press in England and in this country—bumps, in fact, it has very little to do with, being really a science dealing with the measurements of angles and the thinness or thickness of parts of the skull. But at a future time I intend to devote an entire lecture to a subject so prodigal of light upon Man's self-means of education and perfectitude and so certain to give rise to greater progress and greater results. Briefly: in my opinion, the study and application of Phrenology is essential to the civilization of Man.

I must soon conclude; but before so doing I have to remark that I am quite aware that a distinguished Frenchman, Lamarck by name, many years ago suggested that there was a gradual and progressive alteration of animal types, but he founded his ingenious theory entirely on Spontaneous Generation, which I intend to demonstrate in a succeeding lecture has no substantiation, and he (not enjoying the geological, chemical and phrenological advantages that increasing Knowledge has showered on us of the present century) but very imperfectly outlined the subject and did not conceive my principal ideas. I may say the same of the anonymous author of a book called the "Vestiges of the Natural History of Creation" which appeared about three years ago. The book is in some respects a remarkable production and would possess greater merit if its author was not so lacking in scientific knowledge as to place blind faith in a Personal Diety and its benificent planning of the Universe, and to credulously accept the most unlikely tales of animal and vegetable marvels, unconfirmed and poorly vouched for, that one has read outside of the works of Munchhousen and the Brothers Grimm. Both found a lock but neither found its key. Whether I have discovered that key or not, must rest with you and your acquaintances or posterity, Ladies and Gentlemen, to decide—your most careful consideration of what I have set forth being earnestly entreated; for:

"Truth, like a single point, escapes the sight
And claims attention to perceive it right;
But what resembles Truth is soon descried,
Spread like a surface and expanded wide."

THE DANGERS OF THE UNSEEN.

During the few, brief years of our existence in this wonderful world, we sre repeatedly indebted to the constant, the resistless and the enlightening advance of Education for some all too fleeting, yet mind-enlarging, glimpses into the profound, the exhaustless and the enchanting book of Knowledge; that book which, although freely opened unto everyone by the liberal hand of Nature, would have been consumed, annihilated, or at least forever sealed to the curious gaze of priest-ridden Humankind had a bigoted, enslaving and persecuting church possessed the power.

We must not wholly blame the clergy for this would-be wrong. For, in general, it is unthinking Man who wilfully or stupidly places himself in the ready way of his own advancement; who drowns the feeble voices of the gifted few who have something new, instructive, or uplifting to impart for the lasting benefit of him and of his race, with the hiss, the groan, the loud uproar, of the ignorant barbarian; and who in his lamentable shortsightedness casts back the beautiful, naked, mind culturing Truth into the depths of her obscuring well—just as the stern, fanatic, recluse saint thrust the lovely maiden who sought his unresponding love, from the awe-ful precipices of his mountain home lest her too seducing charms should wean him from the austerities, the veneration and the dominion of God and the Church.

Well it is for us that Truth is more than mortal; unlike the poor, feeble girl of the sorrowful legend. Dazzling, pure and fearless, she emerges again, again, and ever, from the depths of crystal clearness as might a twin-goddess—a Minerva-Venus—from her natal wave, each time fairer, stronger and more prevailing; refreshed e'en as the o'erthrown Anteus when, re-invigorated, he upsprang from the bosom of his Mother Earth. Aye, and it is fit that this should be so, for only such incessant, such dauntless, such thought compelling persistence can eventually command the admiration, captivate the mind and impregnate the brain of Thought retarding, God fearing, Church crippled Man; brush the dust from his blinded eyes and disclose to him the majestic thoroughfare stretching grandly out to the shining Temple of Progress, an Olympus the poor dupe who tamely submits to the dark guidance of Religion can never see.

Original Thought, fair thriving child of prolific young Dame Education, has found a deadlier enemy than ever adventurous, valorous, wrong redressing Amadis o'ercame in foul, fire breathing Dragon of the Myths of yore. That foe is Holy Church, whose Titan power, whose Briærius reach and whose Machaivellian craft at one fell period of theworld's sad history almost blotted Intellectuality out of human minds, laid struggling Science on a Cæcus' bed, and infamously halted the sublime march of divine Progress on its difficult but inevitable way.

It is this Original Thought, cradled in some Crichton's brain, that has exquisitely chiselled the civilized (or rather the civilizing) Man out of the rough barbarian; that is irresistibly, openly and enlighteningly overthrowing the Colossus of the Church; and that more and more conclusively demonstrates in the minutiæ of the smallest things it presents to our receptive minds, the potency, the majesty, the unchangeability of the Laws of Nature as luminously contrasted with the impotency, the puerility and the contradictoriness of what is audaciously related of a Biblical personal God.

Original Thought, unaided by sage Experiment, remains but lame Theory—a child in close leading strings—and can be accepted as mature Fact or not, as he to whom it is conveyed, suggested, or expounded chooses to finally decide. But let it be backed by the strong confirmation of Experiment: it then becomes Practical—it is Fact itself, and sooner or later must be received as such by even the most doubting, scoffing and bigotedly oppositional of our obtuse kind.

The Original Thought I wish to put before you tonight may be, I am sorry to say, devoid of as much of the potent aid of Experiment: that is, systematic, directly planned and skillfully conducted Experiment as might be wished. Yet it is a clear expression of Natural, observed phenomena, supported by simple but certain proofs; therefore it presents definite claims to be thoughtfully received as no vagary of Theory, but a substantiality of Fact.

From observation, thought and deduction, I have concluded that earth, air and water are replete with multitudinous, infinitesimal, ever active creatures, probably many of which are too minute for our best microscopes to reveal to the sense of sight. These pigmy, insignificant-seeming and yet collectively formidable beings are everywhere at work—born in myriad numbers, propagating and expiring in a brief season, like May-Flies, ere they hardly have begun to live; they infect or disinfect the air, alter the nature af the soil, and cleanse or contaminate the water. Entering our systems through all of these facile mediums (we inhale on an average about 2800 cubic feet of air through our lungs in the short space of only twenty four hours and swallow dust and water in surprising quantities every day of our lives) they soon obtain mastery over our weakened bodies and it is surely their malefiant effects that we behold in the horrid virulence of small-pox, the dreadful malignancy of cancer and the melancholy ravages of consumption. Kings evil, catarrh, malarial and scarlet fever, measles, the putrid sore throat, gangrene, aye, dozens of other catching ails let loose from a cursed Pandora's box among humankind, are simply the direct or indirect re sults of these almost invisible atoms.

The drop of water we sip, the breath of air we breathe, the particle of dust that finds insidious entrance to our bodies, may be to us the unseen precursor of terrible disease, the unheard knell of fateful doom, the silent fore runner of early, torturing, ghastly death.

Only nearly perfect, very healthy, vigorous bodies can successfully resist these parasitic wanderers, (Ishmael-like roamers through the universe) when they are at their best and we are exposed to their attacks: hence we note a favored few who defy plague and pox and cholera; epidemics of all fateful kinds and remain serene, incautious and unscathed. But woe to the weak, the ailing or the debauched! they fall an easy prey to the fatal onslaughts of these tiny destroyers, everywhere watchful, voracious, insatiate; even as the Harpies of fable or the vulture that preyed on Promo theus. Why this is so, I am unable to say; it is doubtless for the same reason that a stunted, set back, or sickly plant yields to the massed attacks of aphide hosts while healthier close by vegetation of the same kind is nearly free from the vermin destroying the weaker foliage: from what either results, our too scanty store of knowledge avails us not to tell. It may be that, precisely as the spermatozoa, which Leeuwenhoek in 1677 discovered existing in the bodies of men; so other living germs, antagonistic to the evil kinds, may oppose the latter in undebilitated systems and wage war upon the humours in our blood.

I am aware that this mere idea of things such as living atoms produced by the forces of Nature is, in itself, by no means novel.

The wise Aristotle conceived that the mud of rivers might become impregnated with active life by the wizardry of Spontaneous Generation and thus give birth to fishes. Then you will recall to mind the old fable of the bees whom Sampson found abiding in the lion's carcass. Oh how bitterly the church attacked the presumptuous few who first timorously ventured to question the validity of the grounds for this utter absurdity! to deny the statement that neither germs or eggs were necessary for the production of the insects! But the churchmen got a serious set back early in the seventeenth century when Redi laid bare the surpassing fallacy of their claims by making known his justly celebrated experiment with pieces of flesh kept in covered and uncovered jars; and again it tottered when Spallanzani followed in Redi's track with incontestible proof of the continued barrenness of a well boiled infusion preserved from contact with air by a sealed glass vessel. Neither investigator was able to detect the faintest trace of life after long and patient observation. Yet such a man of genius as Lamarck believed in Spontaneous Generation and many others fell in with his views, indeed it required Schwann's truly scientific and masterly researches to finally disprove the plausible theory in 1837, scarcely eleven years ago.

I have repeated most of these interesting experiments and in addition to these have made many more of my own devising. to attempt to now detail which would tediously and uninstructively prolong this, I have no doubt to you, seemingly already drawn-out Lecture.

From them I find that Schwann is, in the main, correct; but further note that the close sealing he has recourse to is unnecessary, merely stuffing the mouth of the containing vessel with cotton wool will answer the same purpose: that of a germ barrier, as the most elaborate sealing if the heated wool is held in a forceps.

A hood dipping into quicksilver answers excellently. Yet mere filtration is inadequate.

I am now certain that this much talked of spontaneous generation is largely a delusion and that if the phenomenon ever does take place it is only exhibited under extremely unusual conditions and in most extraordinary cases. I am also aware that Kircher ascribed the virulence of the Plague to the action of living creatures—you will find his assumption elaborated upon in his scarce and curious "Scrutinum Contagiosæ," published nearly a century and a half ago—but he entirely failed to prove his theory by recourse to experiments (I have made many) and deduce from them many things they made manifest to me.

It is one thing to hint, to guess, to prophesy, but quite another, I assure you, to be able to truthfully say "I know," and then to connect the vague and formless spirit of the Theory with the definite and tangible Matter of Fact.

This I may modestly assert I have done.

I have placed some of the matter containing certain of what I have found to be the minute beings causing the putrid sore throat in the common calves foot jelly so familiar to all of you and covered this with a bell jar standing in quicksilver; jelly, jar and metal all being strongly heated—thus, as you can readily understand, completely excluding any other germs. In three days, these particular germs had amazingly multiplied as rounded jointed grains in wavy clusters, and each little portion of the jelly when placed in pieces of fresh jelly was capable of plentifully propagating them in the new material which, in turn, produced them in others—and so on.

I was curious to see how they would adapt themselves to human blood: to avoid the red color I let some venous stand quietly, having skimmed off some crust; and drew away the greenish yellow watery serum from the cruor and heated it for some hours to 140 degrees of Fahrenheit which I have found sufficient to destroy germ life. In this the beings appeared in only thirty hours! and were larger, fibrous and moist. Other children in the same house with the boy from whose throat I obtained the matter, yielded none of the peculiar germs referred to—until some acquired the same disease, these then exhibited the noxious organisms in his or her greyish throat matter.

Reflection on this, leads us to consider how many diseases may be introduced, transmitted or conveyed by the contact of flesh, perspiration or saliva and how cautious, how prudent and how circumspect we should ever be in governing the intercourse of ourselves and of our children with other persons or creatures, no matter whether the latter appear to be clean and healthy or not. If the system is in proper condition one will go as safely through any contagion as a diver in Halley's suit through the water of the sea, but who is so wise as to know when he is absolutely hale and hearty? one fatal moment of inviting weakness, and wo! the insidious germ has found a foothold.

Then comes the difficulty of dislodgment. These creatures floating numerously through the entire atmosphere and only able to thrive in a congenial harbourage: just as the Tobacco Worm can subsist but on the foliage of the plant from which it receives its name—once having effected this subtle lodgment in our systems, are there protected by phlegmatic or viscid excretions partly emanating, perhaps, from their own organisms and partly consisting of corruption thrown out by the irritated tissues for the purpose of resisting the invasion: as observed in putrid sore throat and in catarrh; and then withstand many substances that otherwise would immediately kill them.

Do not misunderstand me: I do not mean to say that all diseases are thus contracted, but only those that are similar to those I have mentioned. Nor do I assert that the observance of all the precautions hinted at, will ward off all danger. Careful observation has led me to perceive that many of our common insects are conveyers of the germs of illness, disease and death. The House-Fly that crawls over our food or drowns itself in our drink, the Gnat that buries its lancet in our veins, the Bed-Bug that attacks the uncleanly during the slumbers of night, the Wasp and the Bee that thrust us with their stings—all are transporters, injectors or introducers of germ life.

My reasons for affirming this are briefly comprised in the statement that I have never known a person to suffer from malarial fever that had not at one time or other been stung by Gnats or been the resident of a region containing these pests; and that anyone can appreciate the too palpable filthiness of the Fly, feeding, crawling, rioting and breeding in the loathsome repulsiveness of refuse, offal, and decaying abominations of every conceivable kind; then alighting on our victuals or on our persons to trail his defilement over our absorptive epidermis. Doubtless many of you, Ladies and Gentlemen, have seen a magnification of the foot of the Fly, you will therefrom comprehend how easily the wonderfully formed suckers by which this curious creature is enabled to support its own weight in an inverted position, can take up and transfer and impart germs of every description; and you will recognize what extraordinary facilities the insect possesses for acquiring and delivering them.

I suggest that wooden frames be covered with metal gauze such as is used for sieves, and hinged on outside of doors and windows, otherwise, with free access to your houses, what can be safe from the Fly? Oldys, Ladies and Gentlemen, penned a quaint poem on the Fly, bidding the latter "Drink with me and as I;" but I am far from sharing his peculiar poetical sentiments, and I believe that could the "Busy, curious, thirsty" insect be swept altogether out of existence the world would be ever so much the better for it. How to accomplish this, and also annihilate the swarms of Ticks, Fleas, Gnats, Bed-Bugs, and so forth, is indeed a question. Of course cleanliness will effect something towards the desired end; but, perhaps, more than this may be called into play: maybe other creatures can be bred that may abate the numbers of these vermin, just as the Mungoos is used by the Hindu to destroy the Cobra-di-Capello, as the Ferret is set upon the Rat in England and the Ladybird is said to be employed in the South of Europe to exterminate the larvæ of various insects that prey on the poor peasant's scanty crops. Indeed, this is a fascinating, an exhaustless, a labyrinthine subject and could be enthusiastically pursued like Ariadne's silken clue, with infinite benefit to our suffering race. We have an approach to something of the kind in Jenner's valuable vaccine for the prevention of Small-pox. Here, I believe, is shewn a striking instance of the destruction of one germ by another: the substance he employs must contain creatures antagonistical to those of the Small pox pustules, else how could its effects endure so long in the systems of those inoculated with it? And that this, supplied in sufficient quantities, not only overwhelms those of the malady when they enter the blood, but continues to exist, inhabit and breed in that fluid thereby preventing entrance of the other and fatal germ life. If this is so, then what a Sun of Hope—Hope that should "Spring eternal in the human breast" bursts in dazzling splendour on afflicted Man: consumption, cancer, cholera, all must mitigate, recede, or vanish before benificent germs meeting the horrible, destructive causes on their own grim ground and remaining triumphant on the never again to be fought-for field. You may laugh at this, and call it the rosy imagery of a too exuberberant fancy; but let me ask you to observe and notice that things much more incredible have come to pass, aye, and are occurring daily about us, that are now—like the steam engine the great Strassburg clock and the marvellous discoveries in chemistry—so accepted and commonplace as to remain almost unnoticed: what we deem the impossibilities of one age are the actuallities of the next, and I am thus explicit in bringing what I consider is a pregnant truth to your earnest attention because I anticipate the vastness of the fertile field it will surely occupy in the wonderful future which we may never see but which is sure to be.

Now come with me into the seductive realm of the enchantress Theory and reflect upon, debate and analyze the ideas that I have submitted to your attention. May not these invisibles, these atoms of Natural Creation, be the mysterious Absolute of our existence? Of our propagation and decease? Multitudes of these creatures toiling silently in the convoluted brain cells, like the maggots of odd Dean Swift's fancy, may create ideas, intellect, passions. Other legions, laboring in the blood corpuscles, may determine the purity or impurity of that precious medium and, thereby, its vitalizing or devitalizing virtues; while yet other hosts may control (or influence) the decay of our organic structures and their perishable framework? May not soils owe their fertility or sterility, their adaptability or impracticability to the unseen workings of these Genii of the Little? May not water, also, derive many of its properties, beneficial or injurious as they may happen to be, from its teeming contents of microscopical life? We already know (from Bruce, the traveller,) that the natives of far away Abyssinia are infested with parasite Worms through the agency of the water they drink—may not many diseases of the guts originate from germs more minute than these pernicious Larvæ?

All this I believe will be proven to be fact, and in its darker aspect we are very naturally brought to see no hand of God. For what just, compassionate and merciful Father Diety would let loose a host of death dealing, ravenous Wolves in miniature, upon ignorant, frail, supplicating creatures of his kindly creation—his own, fore-known, fore-destined, children? But rather the astonishing, strange uncomprehended workings of some mightier power in almighty Nature infinitely beyond the weak, puny, priest-aborted rudiments of perception, dawning in the infant brain of Man: carrying out a grand design of unfathomable profundity, in which an atom is as mighty as a mass, a second as significant as a thousand years, and the smallest being in the universe of as much importance in the stupendous scheme as lordly Man, himself, with all his presumption, arrogance and self conceit thick upon him—leading us to exclaim with Hamlet, in immortal Shakespeare:

"There are more things in Heaven and Earth, Horatio,
Than are dreamt of in thy philosophy!"

FINIS.

6

[*Extracted from the* PROCEEDINGS *of the* LINNEAN SOCIETY OF LONDON, Session 128, 1915–16.]

PRESIDENTIAL ADDRESS, 1916.

THE HEREDITARY TRANSMISSION OF SMALL VARIATIONS AND THE ORIGIN OF BUTTERFLY MIMICRY.

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A. Introduction.

New and illuminating ideas not only displace much that is erroneous, they unfortunately also tend to disturb much that is true. One old-established truth, as it has been held to be and as I hope to show it to be, forms the subject of the present address.

The evidence for the hereditary transmission of small variations which I propose to lay before you has been yielded by the Lepidoptera, and nearly all of it by butterflies. The special value of the Lepidoptera in the study of variation was strongly insisted upon by A. R. Wallace in his great memoir * read before the Linnean Society on March 17, 1864. The strength and amount of the evidence might, I believe, be indefinitely increased but for the fact that breeders have been led to select the larger rather than the smaller differences as the more conclusive illustration of Mendelian theory, or, from a very different but insistent motive, as more successful in filling their cabinets with striking specimens. But I hope to show that a considerable body of evidence exists, and it is only necessary to direct attention to the fundamental importance of the enquiry to ensure that searching tests will be applied in many directions.

It is to be observed that I am not dealing on the present occasion with heredity as Mendelian or non-Mendelian. I am concerned to prove that small variations are inherited, whatever be the laws that govern their inheritance. I am indeed disposed to think that this address would have been superfluous if serious attempts had been made, with the right material, to answer the question—'what are the smallest variations subject to Mendelian heredity?' One example to be described in later pages (see pp. 25, 26) seems sufficient to prove that they may be very small.

In speaking of Mendelian heredity, I take this opportunity of calling attention to the fact that, shortly before his death, the late G. J. Romanes independently discovered the reappearance of the parental forms of hybrids, in the F_1 generation. I well remember his telling me of the contrast between the uniformity of the hybrids and the sharp division of their offspring into the two parental types *.

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* *Transactions*, vol. xxv., 1866, p. 1. See especially p. 22 and the following passage on pp. 1–2:—"This delicately painted surface [of the wings] acts as a register of the minutest differences of organization,—a shade of colour, an additional streak or spot, a slight modification of outline continually recurring with the greatest regularity and fixity, while the body and all its other members exhibit no appreciable change. The wings of Butterflies, as Mr. Bates has well put it, 'serve as a tablet on which Nature writes the story of the modifications of species.'" See also the present writer's "Essays on Evolution," Oxford, 1908, pp. 50–54, and the references there given.

B. INDIRECT AND DIRECT EVIDENCE OF THE HEREDITARY TRANSMISSION OF SMALL VARIATIONS.

a. *Persistent Variation in two Colonies of a Zygænid Moth on E. Dartmoor.*—This interesting example was observed and recorded † by Dr. R. C. L. Perkins. The colonies of *Anthrocera (Zygæna) trifolii*, which had been observed in four out of the five years ending in 1914, occupied two points on the margin of a pond about 1000 ft. above sea-level. They were separated in the direct line by about 200 yards of water, and the intervening ground along the margin was untenable by the species. Each colony occupied about 15 square yards of boggy ground covered with rushes, in one case intermixed with *Sphagnum* moss. Up to 1914 the colonies were so weak that no specimens were collected, although a difference in variation was noted. In 1914, however, each colony was estimated, from the number of the cocoons which were prominent well up on the rushes, to contain about 100 individuals. The moths from the area with *Sphagnum* are larger, with the red spots on the fore wing distinct or at most the two middle ones confluent. The specimens from the other area are generally of small size, and most of them have "either the three apical spots connected or all are confluent, or the three basal ones. In some the basal part of the hind-wings is yellowish in daylight." The moths are sluggish and are well known to cling year after year to the same small area.

In this example the hereditary transmission of local variation can hardly be doubted; for the *Sphagnum*, not the food-plant of the species, is scarcely likely to be called on as a *Deus ex machinâ*.

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* This was the subject of his exhibit at the Royal Society Soirée on June 15, 1892. The following account, printed in the programme, does not explain the mode of breeding by which he obtained the results described. It is nevertheless implied in these results, and as I have stated he told me of it.

18. *Exhibited by Mr. G. J. Romanes, F.R.S.*

> Living Rats and Rabbits, showing some results of experimental breeding with reference to theories of heredity.
>
> The experiments prove the error of those writers who assume that an act of fertilization consists in the male and female elements intimately blending together, after the manner of a merely mechanical mixture, so that the offspring always presents characters more or less intermediate between those of its parents. In many cases this does happen, but in many other cases the admixture of hereditary elements is by no means intimate—those derived from the father and mother appearing to remain respectively grouped together, with the results shown in the exhibit.

† *Proc. Ent. Soc. Lond.*, 1914, pp. xcv, xcvi. The specimens referred to may be studied in the Hope Department, Oxford University Museum.

The objection may be raised that the variation is large and not small—a matter of opinion which might be discussed indefinitely. It is sufficient for the present purpose to say that the fusion of certain spots in a pattern, or a slight change of tint over part of the surface of a wing are good examples of the kind of variation by which mimetic resemblance has been, in my opinion, perfected.

b. *Hereditary Transmission of Small Variations in the British Moth* Spilosoma mendica.—I owe the two following examples of the hereditary transmission of a very small variation to Mr. A. Bacot, who has kindly presented the material, exhibited to the meeting, to the Hope Department, where it can be studied at any time. Concerning *S. mendica* Mr. Bacot wrote:—"I captured, at Chigwell in 1890, a female specimen of *Spilosoma mendica* which had a small duplication of two of the black dots situated near the hind margin of the fore wings on the upper surface, and also a small spot within the cell near the base of the fore wing. From ova laid by this moth I reared 8 males and 8 females. One male shows the two additional spots near the margin of the wing and also the basal spot; a second male shows, of these markings, only one additional marginal spot, a third male only the basal spot." Nearly all these markings are smaller than in the parent, but all can be distinctly made out with a lens.

c. *Hereditary Transmission of Small Variations in the European Moth* Syntomis phegea.—The second example, referred to by Mr. Bacot in the following paragraph, is even more striking:—

"In a brood of *Syntomis phegea* * that I passed on to you there was an example that had a small but very distinct addition to one of the transparent spots (I think on one side only). I bred from this example, and some of the specimens in the resultant brood showed a similar alteration in the spot. I think that you will have no difficulty in finding the point if you refer to the brood."

The material of the experiment was derived from two males and two females bred in 1899 from Swiss larvæ. From a pair of these was reared in 1900 a family of 17 males and 23 females. The central spot of the fore wing,—the only one in the cell—which exhibited slight variability in the four 1899 specimens, shows a much wider range in the 1900 family. The differences in size are very marked, in fact in one of the females the spots are evanescent. Even more striking is the extent of the unilateral variations, reaching its climax in one male with a semicircular invasion of the black ground-colour obliterating about a quarter of the left-hand spot, while the right one retains the normal size and unbroken squarish outline. Considerable but less marked variations of the same kind are present on the left side of two and the right side of four females, and in a smaller degree in other males and females. In one male with all the spots small, that in the left fore-wing cell is barely visible, although the right is the largest spot in the entire pattern of the specimen.

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* Exhibited, except the 1902 family, by Mr. Bacot at the City of London Entomological and Natural History Society, Feb. 19, 1901. *Transactions*, 1901, pt. xi. pp. 8, 23 (Title only).

Mr. Bacot bred from the male first described and a female which is either lost or at any rate cannot now be identified with certainty. From these parents he reared in 1901 a family of 8 males and 5 females. In three males the spot is large and normal on both sides, in one it is very small on the right, in one very small and divided into two on both sides. The left spots of the remaining three males resemble the male parent in varying degrees: in one it bears a minute central dark spot, in one (A) it resembles the male parent but with a rather smaller invasion, in the third the invasion is much larger leaving only a triangular remnant and a minute dot. The right-hand spots of these three are normal, resembling that of the male parent. The left-hand spot of a single female (B) resembles that of the male parent, the other four being normal or with a slight trace of asymmetry.

Mr. Bacot bred from A and B, rearing in the 1902 family 4 males and 5 females. Of the males, two have much smaller spots on the left, one of them being divided into two; the other two males show only slight asymmetry. Of the females, three show the parental character but in an exaggerated form, the invasion having been carried further, and starting in one of them from the basal margin of the spot instead of its outer margin, as in the others and the parents. A fourth female resembles that last described, except that the invasion is into the right spot instead of the left and has been carried further so that two small dots representing the two outer angles of the spot are all that remain. The fifth female is normal with little want of symmetry.

No one who looks at the material can doubt that this small but striking variation, affecting the shape of a single spot, is hereditary. The series also affords evidence of another kind in favour of the view suggested on p. 22, that Mendelian inheritance will be found to hold in extremely small variations, as well as in large ones. The hind wing in the female *S. phegea* bears two large patches, of which the outer is generally accompanied by a small detached spot lying on its upper (or costal) border. In the male both patches are reduced to spots of which the inner one is especially small and in most individuals represented only by its upper (or costal) section, the lower section when present being minute and quite detached. The evidence bearing on Mendelian inheritance is derived from the presence or absence of the small inner spot in the male hind wing.

Of the two 1899 males, one is normal while the other is as last described, the lower section of the inner spot being much smaller and barely visible on the right side.

In the 1900 family six males are normal, in three or four more the inner spot (upper part only) can be detected with a lens, but in the rest it is altogether absent. There is the most gradual transition from the male in which the inner spot is largest to the one in which it is smallest and can barely be made out with a good lens. The male parent (A) of the 1901 family is without the spot.

Seven males of the 1901 family are normal, while the eighth possesses, in addition to the upper, a distinct lower section. Although the inner spots are transitional in size from normal to very small, none are so minute as to require the use of the lens. The facts strongly suggest that the presence of the inner spot is dominant and that the female parent (B) carried the factors of the normal male. This interpretation is rendered almost certain by the four males of the 1902 family, of which two are without the spot and two with it. Of the latter, one is normal while the other has the lower section as well as the upper, this lower section being in fact better developed than in any other male in the whole of Mr. Bacot's material.

C. Geographical Races or Subspecies.

A large amount of excellent work for many years has been devoted to the study of the differences by which a species is split up into races in various parts of its total geographical range. In Lepidoptera these differences are sometimes large, sometimes so small as to rest upon a slight change in the form or size of a single marking or even the presence of a few coloured scales requiring a lens for their detection. It has recently been argued that geographical races when based on small differences are due to some influence resident in the locality—acquired and not hereditary. Thus Professor Punnett has suggested * that this may be the interpretation of a certain small difference between the Oriental and African forms of *Danaida chrysippus*. During the past few years I have endeavoured to persuade naturalists to breed this butterfly and test whether a high or low degree of development of the character in question—a single spot in the fore wing—is hereditary, and whether the local races will still come true if bred in another country inhabited by another local race of the same species. Up to the present I have not succeeded. The butterfly is so very common that it is difficult to arouse sufficient interest in it. Furthermore it is not always easy to find naturalists who can breed butterflies successfully. But evidence of another kind, yielded by the allied American *Danaida plexippus* (*archippus*), seems to me quite conclusive. Availing itself of modern means of locomotion, the North American race of this butterfly (other races of the same species exist in Central and South America) has during the past 70–80 years been gradually extending its range over the warmer parts of the world. Fortunately it has found its historian in Commander J. J. Walker *, who has recorded its westward migration from 1840 (New Zealand) to 1889 (Straits of Malacca), and eastward from 1863 (Azores) to 1897 (Grecian Archipelago). In many of the localities it has established itself for numbers of years and appears to be now a permanent resident. In spite of all the varying local influences to which it has been subject in its numerous scattered colonies, Commander Walker has never seen a record of any form except the North American one.

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* "Mimicry in Butterflies," Cambridge, 1915, pp. 132–134. See also *Bedrock*, Oct. 1913, pp. 300–301; Apr. 1914, pp. 41–43.

It is unnecessary however to rely solely on experiments made, partly by man who has accidentally transported species to distant lands, partly by nature which has then subjected them to all the strange conditions of the new home. We can appeal to instances in which the whole process has been natural—to local races distinguished by small differences. If now these races, bred in a strange locality, preserve their original differences, the desired test is forthcoming.

I. Direct Evidence of Hereditary Transmission of Local Difference.

a. *Local European and British Races of the Butterfly* Pieris napi *bred in the London District.*—This butterfly, the common English "Green-veined White," has been long known to form local races in various parts of its range. Many of these have been described and named in works on European butterflies. The differences are mainly exhibited by the females but are sometimes fairly well-marked in the males as well. This species has been extensively bred from the egg or from very young larvæ which hatched in transit. by Mr. Hugh Main and the late Mr. Albert Harrison. All the broods were reared at South Woodford, N.E. Mr. Main has kindly drawn up a brief account of the work:—

"Being interested in the local forms, etc., of *Pieris napi*, the late Mr. Albert Harrison and I reared large numbers of this variable insect. Through the kindness of a number of entomological friends we received either living females or freshly deposited ova from a number of different localities in England, Scotland and Ireland, and also from different parts of Switzerland, and from Lapland. From Lapland the female parents were all of the dark var. *bryoniæ*, and we had females of this var. and of the type from different localities in Switzerland.

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* Commander Walker's papers and notes on this species have all appeared in *The Entomologist's Monthly Magazine*, and are as follows:—

(1) "*Anosia plexippus*, L. (*Danais archippus*, F.): A Study in Geographical Distribution." (1886, xxii. 217–224.)

(2) "*Anosia plexippus*, L. (*Danais archippus*, F.) at Gibraltar." (1886, xxiii. 162.)

(3) Observations on the occurrence of "*Danais plexippus*" at Damma, Amboyna, and Ternate. (1893, xxix. 25, 27, 30.)

(4) Observations on occurrence of "*Anosia plexippus*" in New Caledonia, the New Hebrides and the Loyalty Islands. (1902, xxxviii. 192 *et seqq.*)

(5) Observations on occurrence of "*Anosia plexippus*" at Sydney, N.S.W. (1905, xli. 220.)

(6) "The Geographical Distribution of *Danaida plexippus*, L. (*Danais archippus*, F.) with especial reference to its recent migrations." (1914, l. 181–193, 224–237.)

(7) "Some more British records of *Danaida plexippus*." (1914, l. 290.)

(8) "A note on the distribution of *Danaida plexippus* in Australia." (1916, li 294.)

For a brief abstract of the results see *Bedrock*, Apr. 1914, pp. 41, 42.

"In some cases the broods were carried on for two or three years, those from each locality being kept distinct. We always found that each family, though usually exhibiting the wider variability of the species, retained the original general character of the first parents: *e. g.*, the broods from Lapland had a close resemblance to each other, and were very distinct from all the broods from the var. *bryoniæ* females from Switzerland.

"The Lapland specimens resulted from ova despatched by Mr. W. G. Sheldon as soon as they were deposited. The ova generally hatched before arriving in England.

"At Glarus, Switzerland, Dr. T. A. Chapman captured at the same altitude females of var. *bryoniæ* and of the type, which he sent alive. Ova were obtained from several of each, and the progeny of the two forms entirely resembled the parents. All the females resulting from the var. *bryoniæ* ova were of this form, while no *bryoniæ* were produced from ova laid by typical females. The males of both forms I am unable to distinguish from one another. The progeny of the typical females were double-brooded, but only in one family of *bryoniæ* did we obtain any of the summer brood, three females being produced. All the rest of the *bryoniæ* pupæ lay over the winter.

"It is difficult to describe the differences between the various local forms from the British localities, and it would be impossible to separate them accurately if the specimens were all mixed up, but in long series it is seen that there is a strong tendency towards certain extremes which occur in the different places. These strong tendencies are equally evident in the specimens bred from ova deposited in Woodford by females sent from various localities in England, Scotland and Ireland."

The bred and captured specimens kindly lent by Mr. Main, Mr. H. J. Turner and Mr. W. G. Sheldon in illustration of this address entirely bear out the above statements. I especially wish to direct attention to the difference between the Lapland *bryoniæ*, both captured and London bred, and the Swiss *bryoniæ*, both captured and London bred. The two Lapland families and the captured female are smaller and greyer than the commonest Swiss form,—their yellow tint paler and duller, their fore-wing spots smaller and less dark. The close resemblance between 40 *bryoniæ* bred in the London district and their female parent captured in Switzerland is also very striking. Still stronger evidence is afforded by the females of local races from the British Islands, particularly by the specimens bred in London from Irish (Enniskillen) parents. These exhibit the strong black markings and black apex of the fore wing which are characteristic of their locality, most of them too the very pale buff ground-colour which is common there. The London bred specimens from Fife parents afford an interesting comparison, having the markings almost equally well developed, but greyer, and the ground-colour commonly cream rather than pale buff.

In comparing the bred with the captured specimens, the former are of course fresher and the dark markings therefore clearer and sharper. Apart from this there is, Mr. Turner considers, a tendency towards an intensification of the dark markings, especially of the summer brood. Mr. W. G. Sheldon on the other hand considers that the female offspring of Lapland *bryoniæ* exhibit, when bred in England, a reduction of their characteristic features. But allowing all weight for slight effects, probably due to something unnatural in the conditions, it is quite evident that Mr. Main's conclusion is sound and entirely borne out by the extensive material kindly lent by him. Many local races of *P. rapæ* are distinguishable: these differences are hereditary and not acquired. These small variations, many of them exceedingly small, are transmitted by heredity.

b. *Local British Races of the Moth* Aplecta nebulosa *bred in the London District.*—This Noctuid moth is well known to occur in Delamere Forest, Cheshire, in three forms—(1) dark grey forms which are much the commonest; (2) a small percentage very much darker with grey fringes (var. *robsoni*); (3) a much smaller percentage quite black with white fringes (var. *thompsoni*). In breeding (1) behaves as a Mendelian dominant, (2) a heterozygote, (3) a recessive. When bred from the egg in the London district by Mr. Main and Mr. Harrison, not only did the appearance of all three forms remain unchanged, as everyone would expect, but the same was true of a pale local race found in Argyllshire. Examples of these and of the Cheshire forms have been kindly lent by Mr. Main for exhibition.

c. *Hereditary Transmission of Small Variations in W. African Butterflies of the Genus* Hypolimnas.—I here include two examples in the same genus *Hypolimnas*, both due to the careful and accurate work of Mr. W. A. Lamborn in the Lagos district of West Africa. The first is of great importance, because it not only adds to the evidence here summarised but also helps us to understand how two very different mimetic patterns arose. The West African *Hypolimnas dubia* is well known to appear in two forms—*anthedon*, mimicking the Danaine *Amauris niavius*, and *dubia*, mimicking other species of *Amauris*. Mr. Lamborn has shown that these two forms bear a Mendelian relationship to each other, *dubia* being the dominant. Intermediate patterns occur, although in very small proportions, and it might well be supposed that these are heterozygotes and that they would split up in the next generation. Twice, however, Mr. Lamborn has bred from a slightly intermediate (viz. tending slightly towards *anthedon*) female *dubia*, and the pattern of both was strongly inherited by the *dubia* forms among the offspring*.

The second example is *Hypolimnas dinarcha*, of which Mr. Lamborn bred two large families from known female parents. In one of these the white of the hind wing is faintly tinged with yellow and there is a very slight difference in the pattern of the fore wing. There is a strong tendency towards the inheritance of both these features by the female offspring †.

d. *Hereditary Transmission of Small Variations in the* Hippocoon *Female of the African* Papilio dardanus.

The inheritance of small variations in the pattern of the black and white *hippocoon* females of *Papilio dardanus* has been carefully studied by Dr. G. D. H. Carpenter ‡, who has shown that a single small spot in the fore-wing cell differs in size in various parts of Africa and also that slight differences in this and other features between the females in the same locality are inherited by their *hippocoon* offspring. Some of these differences are excellent examples of small steps that would lead towards the transformation of the *hippocoon* pattern characteristic of one part of Africa to that which, under the influence of a slightly different model, is characteristic of another part §. Dr. Carpenter's paper is a complete answer to the contention that, in no clear case, has the inheritance of any small variation been shown to exist ‖.

II. Indirect Evidence of Hereditary Transmission of Local Difference.

a. *The V-Mark on the Hind Wing of the Danaine Genus* Tirumala.—I now propose to consider certain indirect evidence of the hereditary transmission of small variations. Of this an unlimited amount is yielded by a study of the geographical changes in the patterns of related groups of species or subspecies. In passing from one locality to another across the total range we are constantly made aware of extremely minute progressive differences only to be reasonably explained by the gradual disappearance or modification of a relatively ancestral feature highly developed or differently developed in some other part of the common area of distribution. When at some widely separated locality the progressive changes first culminate in the disappearance of the feature, this climax of modification may only be found in relatively few individuals, the others still retaining traces varying from a few scales or even a single scale up to a small but distinct representation. A little further, and the proportion of entire disappearances increases while the size of the maximum representation decreases. Thus by progressive changes in the average constitution of the mass of individuals in successive geographical zones the complete disappearance of the feature may be finally reached.

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* Recorded in *Bedrock*, Apr. 1913, p. 56, plate iii.; Oct. 1913, pp. 299, 300.

† *Bedrock*, Oct. 1913, p. 300.

‡ *Trans. Ent. Soc. Lond.*, 1913, p. 656.

§ The significance of one of these hereditary features was pointed out by the present writer in *Bedrock*, Apr. 1913, p. 50.

‖ Professor Punnett in *Bedrock*, July 1913, pp. 152, 153.

The Oriental species of the Danaine genus *Tirumala* possess * a very distinct V-shaped mark at the inner end of area 2 of the hind wing, in the acute angle between vein 2 and the cell. Most of them have also a smaller mark of the same form at the inner end of area 3. One African species of the genus, *T. petiverana*, barely distinguishable from the common Oriental *T. limniace* or *T. septentrionis*, possesses the V-mark fully developed. Three other species, one of them separable into two subspecies, evidently represent a much earlier invasion, and are greatly modified—so much so indeed that Moore placed them in a separate genus, *Melinda*. I thought it would be of interest to study the fate of the V-mark in these four forms, of which two are East African and therefore near the original home, one Central, and one Western. In addition to specimens in the Oxford University Collections, I have been enabled, by the kindness of Lord Rothschild, to examine material from Tring. The result of the enquiry is shown in tabular form below.

Degrees of development of the V spot on hind wing upper side of four African forms of the Oriental Danaine genus *Tirumala*.	I. The V with the longer limb from 3·0 mm. to 3·5 mm. long.	II. V reduced to a solid arrow-head with longer side about 1·5 mm.	III. Similar to II but length 0·5–1·0 mm.	IV. A minute trace, varying downwards from a recognisable apex to a barely visible spot.	V. No trace visible, even with lens.
1. *T. formosa neumanni*, Rothsch. Abyssinia.	4 ♂ 1 ♀	2 ♂	8 ♂	3 ♂	1 ♂
2. *T. formosa formosa*, Godm. British and German East Africa.	6 ♂	9 ♂ 1 ♀	15 ♂ 3 ♀	10 ♂ 4 ♀[1]	2 ♂ 2 ♀
3. *T. mercedonia*, Karsch. Uganda.			3 ♂[2]	2 ♂[3]	39 ♂ 20 ♀
4. *T. morgeni*, Honr. Cameroons.			1 ♂[4]		1 ♂ 1 ♀

[1] The trace on L. side only of one ♂, R. only of another and of one ♀.

[2] The mark of the value of III on R. side, of IV on L. of one of the three males.

[3] The trace apparently represented by a single pale scale on L. side only of one of the two males.

[4] A very minute III. The pale tint much dimmed and not bright as in the other forms 1–3.

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* *T. neptunia* of Fiji has lost this mark on the upper surface, retaining a trace below. The change is part of a general darkening in mimicry of local Euplœas.

The facts set forth in the above table are best explained by the strong endurance of a hereditary feature gradually weakened as the African invaders became further and further separated from the original stock where the feature is prominent in all the species I have examined except *T. neptunia.* I do not myself doubt that the weakening has been brought about by the selection in *mercedonia* and *morgeni* of individuals which approached most nearly to the pattern of the indigenous African Danaines of the genus *Amauris*; but from the present standpoint I am only concerned to point out that the existence side by side in the same locality of individuals with a minute trace of the mark and individuals with no trace at all, and the comparison of these with the individuals of allied forms in other localities, cannot be reasonably explained except on the supposition that the degree of development of the feature is hereditary. And the different degrees distinguished in the table on p. 31 are *very* small variations.

b. *Geographical Changes in Mimetic Species corresponding with a Change of Model.*—Under this head a large body of evidence is available in support of the conclusion that mimetic patterns arose by successive stages, and not suddenly as Professor Punnett maintains—evidence which at the same time is available for the general conclusion that small variations are hereditary. The limits of time and space prevent anything more than the discussion of one good example from Africa and another from S. America.

c. *The Mimetic Females of the African* Charaxes etheocles.—A wonderful example of geographical change in a single species is seen in the mimetic females of *Charaxes etheocles*, which in various parts of Africa mimic the females and sometimes the males of the larger species of the same genus. Among these local changes are some which are quite as small as the steps by which I believe that an elaborate mimetic pattern has been built up, and it is as certain that these small variations are hereditary as that any geographical race is permanent and fixed. It might indeed be argued by one who has not compared the specimens, that each mimetic female form in each locality had developed from the same ancestral pattern. The following examples, to which others might be added, afford evidence that the female forms are not thus evolved separately but by the modification of those in adjacent areas.

The female form *viola*, of the West Coast, possesses a broad orange bar beyond the middle of the fore wing and a still broader white one shot with blue beyond the middle of the hind wing. This form is believed by Dr. Karl Jordan to be a rough mimic of *Charaxes epijasius.* In parts of British East Africa and of Uganda the model is the male of *Charaxes ansorgei* and in correspondence with its pattern the bars of both wings are, in the form *kirki*, more centrally placed and duller, that of the hind wing narrower. In the Taveta district of British East Africa, as was recorded by the Rev. K. St. Aubyn Rogers [*], the model is *Charaxes saturnus*, and the hind-wing bar of the mimic has become clouded with orange-brown to a varying degree in different individuals, while the fore-wing bar has broadened and tends to suffuse the dark ground-colour.

d. *A South American* Heliconius *Mimetic of another Species of the same Genus.* —This example is of great interest inasmuch as it was detected in the fine and abundant material collected in Brazil between 1825 and 1830 by W. J. Burchell. Furthermore, the specimens are accompanied by statements, in the handwriting of Professor Westwood and of Burchell himself, which prove that the variation is so small that it escaped their attention altogether. The material consists of a series of dark brown nearly black butterflies, bearing on the fore wing, beyond the cell, a broad red bar, and, between the bar and the base, a median narrow yellow stripe; on the hind wing, a broad and conspicuous yellow stripe. All the specimens had been labelled with Burchell's customary care and precision, and on a slip of paper attached to one of them, taken Mch. 10, 1826, at Rio de Janeiro, Westwood wrote—"69 individuals in full of this species without any variation of the least importance taken bet^{n} 24.10.25 [†] & 24.3.29. See list in my Burchell Catalogue." Opposite the list of dates copied from Burchell's labels into the catalogue above referred to, Westwood wrote "*Hel. Phyllis.* 69 ind^{s}" When a list of Burchell's Heliconinæ was prepared for publication [‡] by Mr. E. G. Joseph, B.Sc., a few years ago, 61 specimens out of the 69 were found in the Hope Department, but of these one had lost its label. Fifty-four of the 60 are the abundant Fabrician species *Heliconius erato phyllis*, 42 from the vicinity of Rio de Janeiro (Aug. 16, 1825—1; Dec. 6, 1825–Apr. 1, 1826—41); 10 from Minas Geraes (Oct. 14, 1825–Nov. 7, 1825); 1 from Santos (Sept. 19, 1826); 1 from Goyaz (Apr. 30, 1828). The 6 remaining specimens belong to two subspecies of the Opisogymni, a section of the genus different from that which includes *erato phyllis.* The latter belongs to Stichel's Section II, the Opisorhypari, in which the males are distinguished from those of Section I, the Opisogymni, by a narrower glistening area on the under side of the fore wing where it overlaps the hind. The Opisorhypari are as a rule the most abundant of the Heliconians and they are commonly mimicked by those Opisogymni which enter their areas of geographical distribution. A single one of the remaining six specimens is *Heliconius nanna,* captured by Burchell together with two of its models, *H. erato phyllis*, on Dec. 6, 1825, "in an excursion to the summit of the Corcovado," near Rio. At first sight the model and the mimic are so precisely alike that we do not wonder at Westwood's statement that the whole series was "without any variation of the least importance"; but with a closer examination it is at once seen that the red bar of *erato phyllis* is sharply outlined while that of *nanna* is gradually transitional into the dark ground-colour. Thus one of the six Opisogymni is accounted for: the remaining five, all taken Mch. 2–24, 1829, at Porto Réal (Porto Naçionale) on the Tocantins River, came from outside and to the north-west of the area in which Burchell captured *erato phyllis.* All the dates in Westwood's catalogue are here to be found on the specimens, so that nothing is missing from this part of the collection. These five examples, although with a softly outlined red bar, are easily distinguishable from *H. nanna,* and if Professor Westwood had arranged the individuals geographically he would certainly not have maintained that the variation was without the least importance. For directly a geographical arrangement is made there separates out this little group of 5 individuals with patterns all very much alike, and all differing from those of the 55—54 models and 1 mimic—collected in another area lying to the south and east. In these 55 the lower outer border of the broad red bar is produced into two strongly marked projections or teeth. The same border in the 5 individuals from the north-west bears only the lower projection and this shortened and rounded. Examples in the collections of the British Museum and Mr. W. J. Kaye agree with those collected by Burchell. The difference is distinct but it is small—so small indeed that it had not only escaped the attention of Westwood in the museum but also of Burchell in the field; for the latter had noted concerning a specimen taken at Porto Réal on Mch. 2, 1829: "*Papilio.* The brown-winged (*Horta* *) with a red patch on the upper wings, is always found in shady woods and forests. I have seen it in similar situations in every part of Brazil I have visited." These words indicate that he looked upon all the specimens as belonging to a single species. But the difference, although small, is constant and forms the distinguishing feature of the north-western subspecies *H. nanna burchelli.* From this form there can be no doubt that *nanna nanna* has been produced to the east and south under the influence of the extremely abundant *H. erato phyllis.* Dr. H. Eltringham has shown in a paper † which will appear in the Transactions of the Entomological Society for the present year that the male genitalia of the two races are precisely similar although very distinct from those of *erato phyllis*, and he also agrees that *nanna* certainly arose from *burchelli* and not *vice versa.* We have then an excellent example of the origin of a mimetic form by means of a variation in pattern so small as to deceive two extraordinarily observant naturalists, an example which at the same time provides evidence that small variations may be hereditary. This latter conclusion can only be escaped by assuming that the constant differences between these local forms are due to some unknown local influence and not transmissible by heredity. But Dr. Eltringham has shown in the memoir already referred to that both *nanna* and *burchelli* are only two out of a long list of geographical races into which *Heliconius melpomene* is split up, some of them with wide differences in pattern, some with small. Probably everyone would agree that the larger differences are of germinal origin and hereditary; yet large and small are all local races indistinguishable by the structure of the male genitalia. The onus rests upon those who would put them in different categories.

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[*] *Trans. Ent. Soc. Lond.*, 1908, p. 507, n.

[†] This date is erroneous. The earliest date in Westwood's catalogue and on the specimens is 16.8.25. There are also other dates earlier than 24.10.25.

[‡] *Ann. Mag. Nat. Hist.* ser. 8, vol. v., Apr. 1910, p. 322.

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* It is shown, in *Ann. Mag. Nat. Hist.*, 1910, pp. 333–5, that by "*Horta*" Burchell meant to imply a place in the Fabrician "Heliconii."

† "On Specific and Mimetic Relationships in the genus *Heliconius*, L." *Trans. Ent. Soc. Lond.*, 1916, pp. 101–148, plates xi–xvii.

E. B. P., Sept. 4, 1916.

D. The Origin of a Mimetic Pattern.

The inheritance of small variations is closely connected with the problem of the origin of mimicry. Without such inheritance a likeness cannot have been gradually improved, and we should have before us no solution except that which assumes the sudden origin of an elaborate pattern resembling in wonderful detail that of some remote species. Such a solution has been proposed within the last few years, and it will be well to consider some of the difficulties which it encounters.

a. *A Mimetic Pattern supposed to arise suddenly from a set of Factors similar to those which produced the Pattern in the Model.*—This suggestion was first made by Professor Punnett, who maintained that on the Mendelian view "the genera *Amauris* [the Danaine model] and *Euralia* [the Nymphaline mimic] contain a similar set of pattern factors, and the conditions, whatever they may be, which bring about mutation in the former lead to the production of a similar mutation in the latter" *. This interpretation, although it does not carry us very far, has been accepted as satisfactory by some writers †. When it was pointed out that the patterns of model and mimic are only superficially alike and that, to name one obvious difference, the markings of *Amauris* were hard in outline and those of the mimetic *Euralia* (*Hypolimnas*) soft ‡, Professor Punnett replied that "it is not unreasonable to suppose that these species carry identical factors for colour pattern, and that the differences by which the eye distinguishes them are dependent upon the minuter structural differences such as occur in the scaling. So the eye would distinguish between a pattern printed in identical colours on a piece of cretonne and a piece of glazed calico. Though pattern and colour were the same the difference in material would yield a somewhat different effect"[*].

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* "Mendelism," 1911, pp. 134, 135.

† See for example the review by Francis B. Sumner in *Journ. Philos.*, New York, vol. ix. pp. 159–161.

‡ *Bedrock*, Apr. 1913, pp. 52, 53.

The chemical nature of the colours of butterflies has not been much investigated, except in the *Pierinæ*, where the white, yellow, orange and red pigments of the mimics have been shown by Professor F. Gowland Hopkins[†] to be quite different from those of their models. But even without chemical analysis it is clear that the red of a *Pharmacophagus* swallowtail model is very different from the red of its *Papilio* or *Cosmodesmus* swallowtail mimic. Thus Professor Punnett, alluding to the quality of the red in the models of the two mimetic *Papilio polytes* females says: "in both models it is a strong clamorous red suggestive of a powerful aniline dye, whereas such red as occurs in the mimics is a softer and totally distinct colour"[‡]. Hence in these two large classes of mimics, Pierine and Papilionine, the suggestion of identical factors in model and mimic cannot apply.

A critical examination of other models and their mimics constantly reveals difference under the apparent sameness of colour and pattern. I will mention a single example because it illustrates a physical rather than a chemical difference. Mr. S. A. Neave has told me that the semi-transparent white markings on the black and white species of the African Danaine genus *Amauris* appear blue when the insect is on the wing, an effect that can be witnessed by holding an opaque black surface beneath the pattern. It is not due to pigment but to the structure of the scales. Such a mimic of *Amauris* as the *hippocoon* female of *P. dardanus* only reproduces this effect very feebly, but the *Hypolimnas* (*Euralia*) co-mimics—e. g. *H. anthedon* in the west, and *H. wahlbergi* in the east—exhibit it strongly and in a form somewhat different from the model. The blueness is here in part due to a delicate iridescence of the white scales very similar to that of the *Amauris*, but also to intensely blue marginal scales, absent from the Danaine model, but common to many species of *Hypolimnas*, including the non-mimetic males of mimetic species and both sexes of the huge *H. dexithea* of Madagascar. The ancestral material of the genus *Hypolimnas* has been worked up into the mimetic likeness to a model which does not possess such material at all.

Assuming, however, for the sake of argument, that mimics exist in which the chemical and physical causes of colour are identical with those of their models[§], it is important to enquire whether Professor Punnett's metaphor of patterns on cretonne and calico really help to explain the facts or only to disguise an essential difference.

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[*] "Mimicry in Butterflies," Cambridge, 1915, p. 148.

[†] *Proc. Roy. Soc.* lvii. 1894, p. 5; and *Phil. Trans.* 1895, B. p. 661.

[‡] "Mimicry in Butterflies," p. 82.

[§] Instances doubtless occur where model and mimic are closely allied, as in the *Æneas* and *Lysander* groups of *Pharmacophagus* or the well-known convergent Danaine or Acræine groups.

b. *The Edges of Markings in the Patterns of Models and their Mimics.*—With certain exceptions—unimportant from our present standpoint—the pigments * of butterflies' wings are contained in the scales. Two colours do not occupy the same scale, but the passage from one colour to another is effected by a set of scales containing one pigment being replaced by a set containing another. In the examples referred to by Professor Punnett in the passage quoted on pp. 35, 36, the yellow scales are suddenly replaced by black scales at the margin of the hind-wing patch of *Amauris echeria*, while they are not suddenly replaced in the mimic, the *mima* form of *Hypolimnas dubius*. A part of the area that is wholly yellow in the model contains abundant scattered black scales in the mimic and so with part of the black area which in the mimic contains plenty of yellow scales. Scales that are yellow in the one are black in the other and *vice versa*. The difference is real.

The metaphor is also misleading in another way: it seeks to explain the difference as an incidental outcome of specific constitution unconnected with mimicry. But the soft outline is a common characteristic of the mimetic pattern just as the hard outline is of the model's. The *Hypolimnas* mimic is far more closely allied to the Danaine model *Amauris echeria* than either of them are to the Papilionine mimic, *P. dardanus*, yet both mimics exhibit the soft-edged pattern. They exhibit it in fore wing as well as hind: they exhibit it in all their other forms mimetic of other comparatively hard-outlined Danaine models. The following sentence, published by the writer fourteen years ago, refers to the most conspicuous and best-known black and white model and mimics in Africa:—". . . The white centre of the upper surface of the wings deepens gradually at its margin into black in both Papilio and Nymphalid, while the margin of the corresponding white area in the Danaine exhibits an extremely sharp and abrupt transition into black" †.

These differences between the edges or borders of markings on butterflies' wings are important and I propose for them the terms *eulegnic* (with a clear edge), and *dyslegnic* (with a dim or bad edge), the latter passing into *alegnic* (without an edge), kindly suggested to me by Professor Gilbert Murray ‡.

c. *Modes of Occurrence of Dyslegnic Patterns in Butterflies.*—Dyslegnic patterns are not only common in mimics as compared with models, but are also common in females as compared with males. Thus the mimetic female forms of *Papilio dardanus* bear in this respect the same relation to their Danaine models that they bear to their own male, and the female of the non-mimetic ancestor *P. meriones* in Madagascar is also far less eulegnic than its male. The dyslegnia has preceded the mimicry. If the brighter colours of male butterflies have been developed by sexual selection—and the fact that male brilliancy is due to interference colours as well as pigments strongly supports the Darwinian interpretation—it is also highly probable that their more eulegnic patterns have arisen in the same way.

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* The same argument applies to the physical causes of colour here omitted from consideration for the sake of simplicity.

† *Trans. Ent. Soc. Lond.*, 1902, p. 486, n. The passage refers to the hind wings of the western Danaine *Amauris niavius* and of its two mimics the *hippocoon* female form of *Papilio dardanus* and both sexes of *Hypolimnas (Euralia) anthedon*, also to the corresponding eastern and south-eastern forms—*A. niavius dominicanus*, *hippocoon* (or *hippocoonides* as it has been called in this area), and *H. wahlbergi*.

‡ λέγνον, an edge or border, with the prefixes ἐυ- good, δυσ- bad, or α- not.

When the sexes of a mimic are alike the male pattern as well as the female tends to be dyslegnic. This is commonly true in both sexes of the mimetic swallowtails of the section *Cosmodesmus*, as it is of the mimetic females of *Papilio*. An excellent example has already been described in the fore wing of *Heliconius nanna* with both sexes alike (p. 34).

In order to test the prevalence of dyslegnia in mimicking butterflies, I examined a considerable series selected many years ago as illustrations, and without any thought of this characteristic. Everywhere in the series the mimics were dyslegnic as compared with the models *. They included Nymphalines of various genera and Papilios of various species mimicking Danaines, Nymphalines mimicking Acræines, and *Acræa natalica* mimicking *A. anemosa*. The principle was commonly manifested by the Papilionine mimics of the *Pharmacophagus* Papilios of which a long illustrative series has been arranged in the Hope Department. One of the most striking examples is provided by the strongly dyslegnic patterns of all the forms of *Elymnias*, mimicking Danaine and Pierine models in the East and Acræine in Africa.

Having thus examined a number of well-known examples I thought it would be interesting to apply the test to newer instances only recently worked out in detail. Accordingly the attempt has been made to set forth in tabular form (Appendix, p. 51) the condition of the pattern edges in a series of similar patterns belonging to the two sections of the *Heliconinæ* referred to on p. 35. The series itself is fully described and illustrated in Dr. Eltringham's memoir† on the *Heliconinæ* now in the press and to appear shortly in the Transactions of the Entomological Society for the present year. Dr. Eltringham has kindly read the tabular statement and confirms the descriptions. Mr. W. J. Kaye, with a wide experience of the relative abundance of the forms in the two sections, has kindly added the notes which express what is known on this point. The table shows that on the whole the forms of Section I are more dyslegnic than those of Section II, but that one common feature in the pattern, the yellow bar of the hind wing, is generally eulegnic and often more so than in Section II. Now this bar is shown by Dr. Eltringham, for reasons which do not apply to Section II, to be probably ancestral in Section I. It must further be added that Dr. Eltringham shows that, with the possible exception of *H. pachinus*, all the forms in Section I mentioned in the Appendix are the races of a single species, and that the same is true of groups of forms in Section II such as the races of *H. erato* and *sappho*. Such evidence of recent change being common in Section II as well as I renders the table less applicable as a test of dyslegnia in relation to mimicry.

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* The only exception that I encountered was the alegnic transition from orange-brown to black in the fore wing of *Danaida chrysippus*. In this butterfly and its mimic, the female *Hypolimnas misippus*, this transition appears to be real, being brought about by a gradual darkening in the colour of the pigment in the scales as the black area is approached—not by the "stippling" of the usual dyslegnic margin. In other respects the pattern of *D. chrysippus* is eulegnic (see p. 42). It is interesting to note that this alegnic transition from orange-brown to black is associated with extraordinary variability in the relative areas of the fore wing occupied by these two shades.

† See Note † p. 34.

The facts in these *Heliconinæ* support the conclusion that the dyslegnic pattern is commonly found where there has been recent change as shown by close relationship with other forms, exhibiting slightly different patterns. Of course I do not assert that the eulegnic pattern never changes, only that dyslegnia is the usual accompaniment of change. Thus the Danaine model *Amauris niavius*, so often alluded to, has a pattern which is eulegnic except below the hind-wing cell; this is just the part which undergoes change, the border which advances, producing an immensely larger white marking on the east coast. Not only these, but the western race with a comparatively small patch and individuals from the east of the Victoria Nyanza with an intermediate patch, are all dyslegnic along the corresponding border. On the other hand the small spot in the fore-wing cell remains eulegnic throughout although it too increases in size on the east. But this is an extremely small change as compared with the other.

The dyslegnic pattern is also commonly found in single aberrations and in vestigial spots and markings. It predisposes to change and tends to persist as a register of change. It is often correlated with another predisposing cause of change—variability of colour.

E. FEMALE MIMICRY *.

It is here well to reprint the whole of a passage of which the latter part is as a rule only quoted. On p. 22 of his great paper (1865) Wallace, after describing the mimetic likeness of the females of certain Eastern Papilios to other presumably specially protected Papilios, continues :—

"The last six cases of mimicry are especially instructive, because they seem to indicate one of the processes by which dimorphic forms have been produced. When, as in these cases, one sex differs much from the other, and varies greatly itself, it may happen that occasionally individual variations will occur having a distant resemblance to groups which are the objects of mimicry, and which it is therefore advantageous to resemble. Such a variety will have a better chance of preservation; the individuals possessing it will be multiplied; and their accidental likeness to the favoured group will be rendered permanent by hereditary transmission, and, each successive variation which increases the resemblance being preserved, and all variations departing from the favoured type having less chance of preservation, there will in time result those singular cases of two or more isolated and fixed forms bound together by that intimate relationship which constitutes them the sexes of a single species. The reason why the females are more subject to this kind of modification than the males is, probably, that their slower flight, when laden with eggs, and their exposure to attack while in the act of depositing their eggs upon leaves, render it especially advantageous for them to have some additional protection. This they at once obtain by acquiring a resemblance to other species which, from whatever cause, enjoy a comparative immunity from persecution."

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* See also the author's "Charles Darwin and the Origin of Species," London, 1909, pp. 132–9.

In the earlier part of this passage Wallace clearly emphasises the rôle of female variability in the origin of female mimicry in butterflies, and later work tends to emphasise it still further. Considering such a common non-mimetic species as *Terias hecabe*, we find the bright eulegnic constant male is associated with a female having duller colours, dyslegnic pattern and much greater variability. Furthermore, the study of families with known parents bred by Mr. E. E. Green in Ceylon supports the conclusion that the degree of variability is hereditary. It is clear that the change to a new pattern would be far more likely to occur in the female of *Terias hecabe* than in the male, and that the particular kind of variability which I have called dyslegnia conduces to such a change. *Charaxes etheocles* affords another example. The females of this species mimic the females and sometimes the males of other larger species of *Charaxes*. I have recently received from S. Nigeria several specimens bred by Mr. W. A. Lamborn and by Mr. C. O. Farquharson; the females of these are non-mimetic and only differ from their males in the possession of an extremely obscure, unstable and highly dyslegnic pattern in paler tints dimly visible on the dark background of the wings—nevertheless, slight as it is, the expression of female variability.

Terias hecabe is an example of a species in which the sexes are nearly alike; when we consider those in which they are widely different the origin of female mimicry becomes much clearer. The most striking example known to me was brought to my notice by my friend Mr. S. A. Neave. I refer to the African Nymphaline butterfly, *Precis westermanni*, with an extremely constant male, although the pattern is somewhat dyslegnic, and a female varying in different directions with patterns of several kinds sometimes clearly, sometimes dimly suggested. There are orange-brown forms like the *dorippus* form of *Danaida chrysippus*, orange forms with dark fore-wing markings like *Precis sophia*, forms with dark fore wings—sometimes again shot with a purplish iridescence—and orange black-spotted black-margined hind wings, similar forms with varying amounts of white and of orange in the fore wing and of white in the hind; finally, forms in which this white invasion is so extreme as to form a broad continuous bar crossing both wings. Furthermore there are immense differences in the breadth and the pattern of the dark margin of both wings. Here is a butterfly which seems to present ready-made, in the material afforded by female variability, the foundation of half a dozen different mimetic patterns.

A much less striking but still convincing example of the importance of female variability in the origin of mimicry is offered by *Pieris napi* described on pp. 27–29. Here the possibility for the development of new patterns is obviously much greater in the variable female than in the constant male.

A good example of an undoubted but very imperfect mimic—such a mimic as might easily arise from almost any of the female forms of *Precis westermanni*—is afforded by a form of *Pseudacræa albostriata* common, although not so abundant as the typical non-mimetic form, in the Entebbe district of Uganda. This local form with its white-barred hind wing and orange-red marked fore wing is clearly an outlying member of the great assemblage of mimics clustered round the powerful Acræine models *Planema poggei* and the male of *P. macarista*. I have only recently realised that it is an evident secondary mimic of another outlying mimic of the Planemas, the male of *Acræa althoffi*. In *Pseudacræa albostriata* both sexes are highly dyslegnic, but the female more so than the male; both have produced the local mimetic form, but the female's is more perfect than the male's. This too was only recently determined when all the best mimics were selected from the series collected by Mr. Neave, and it was found that they were all females and that those left behind were all males. The sex-linking here is confined to the degree of variation and does not involve its kind. The male and female are on the same path but the female keeps a little ahead.

F. Polymorphic Mimics and the Origin of Mimicry.

One of the most interesting and indeed exciting developments of butterfly mimicry in recent years is the immense increase in our knowledge of single species with many polymorphic forms resembling a number of models belonging to different species. The firm and solid foundation of this development lies far back in the three great monographs by Bates, Wallace, and Trimen, published in our Transactions in 1862, 1865, and 1869 *. But wonderful as was the discovery of the polymorphic mimetic females of Oriental Papilios by Wallace and of the African *Papilio dardanus (merope)* by Trimen, naturalists were certainly unprepared for the astonishing polymorphic mimicry of both sexes in the African forms of *Hypolimnas* proved by Millar, in the still more wonderful forms of the African *Pseudacræa eurytus* proved by Jordan and confirmed by breeding by Carpenter, and in the S. American Heliconine forms mentioned in the Appendix (p. 51) and proved to be conspecific by Eltringham. In all of these the transitional relationship between the patterns in each set of polymorphic forms can be traced and the conclusions based on pattern brought into line with those based on structure and on breeding. No such relationship exists (except in some of the *Heliconinæ*) between the patterns of any of the different species which contribute the set of models for each group of polymorphic mimics, and the whole series of facts strongly opposes Professor Punnett's hypothesis of the mutational origin of mimicry from a set of factors identical with those which produce the pattern of the model.

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* The two latter papers are often quoted as published in 1866 and 1870, the dates of the *volumes* in which they appear, but the *parts* were issued in each case in the previous year.

I propose now briefly to consider the best known and most striking of the much rarer cases in which the models as well as their mimics are polymorphic; for here if anywhere in polymorphic mimicry we should expect to find evidence in favour of Professor Punnett's hypothesis. I refer to *Danaida chrysippus* with its three forms *chrysippus*, *alcippus*, and *dorippus*, all of which are well known to be mimicked in Africa by the female of *Hypolimnas misippus*, and by both sexes of *Acræa encedon*, while the first and last are mimicked by two forms of a *Mimacræa* (*Lycænidæ*) probably belonging to the same species. Here then are three forms of a model mimicked respectively by three forms of the female of one mimic and both sexes of another. It might be expected that the latter at any rate, for the model also is polymorphic in both sexes, would present the essential similarity due to the appearance in both of the same pattern factors. But as I pointed out in 1902 * the different forms of *chrysippus* are far more sharply separated from one another than those of its mimics. All three of the latter show a much wider range of pattern variation and especially of transition between their polymorphic forms. And this is conspicuously evident in *Acræa encedon* with both sexes polymorphic. Accompanying these characteristics of the mimetic pattern there is the usual dyslegnia, while the model is eulegnic except in the feature described on p. 38, Note *.

a. *Polymorphic Forms, — Mimetic Constant and Non-Mimetic Variable,—in the Same Species.*—In another respect recent discoveries in the polymorphic mimics throw light upon the origin and growth of mimicry, strongly supporting the Darwinian interpretation. Thus Dr. Carpenter has shown † that in certain islands in the N.W. of the Victoria Nyanza where for some reason the mimics are much commoner than their models, intermediates

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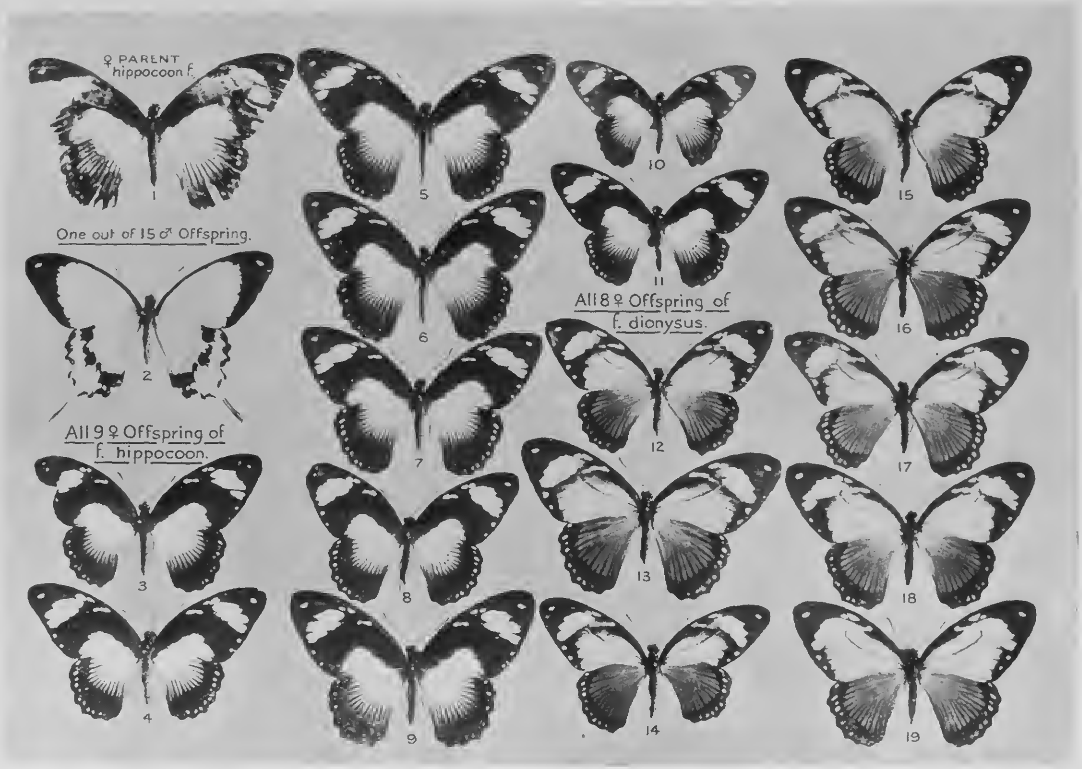
* *Trans. Ent. Soc. Lond.*, 1902, pp. 483, 484.

† *Trans. Ent. Soc. Lond.*, 1914, pp. 606–645.


♀ PARENT
hippocoon f.
1
One out of 15 ♂ Offspring.
2
All 9 ♀ Offspring of f. hippocoon.
3
4
5
6
7
8
9
10
11
All 8 ♀ Offspring of f. dionysus.
12
13
14
15
16
17
18
19

Alfred Robinson, photo.

Papilio dardanus. Family bred by W. A. Lamborn in S. Nigeria (1913) from *hippocoon* ♀ parent (Fig. 1), including one ♂ (Fig. 2) out of 15, and all ♀ offspring 9 *hippocoon* (Figs. 3–11), mimicking the dominant Danaine *Amauris niavius*, constant; 8 *dionysus* (Figs. 12–19), without a model, variable. ⅔ of natural size.

between the forms are much commoner than on the adjacent mainland of Uganda where Mr. C. A. Wiggins has shown * that the models are more abundant than the mimics. No reasonable interpretation has been suggested except the one proposed by Dr. Carpenter—that natural selection operates more stringently in the preservation of the mimetic forms in one area than in the other. Confirmation of a remarkable and striking kind has been obtained by Mr. W. A. Lamborn †, who in 1913 bred from a black-and-white *hippocoon* female of *Papilio dardanus*, captured near Ibadan in S. Nigeria, the female offspring all of which are represented in the accompanying plate I. Of the 15 male offspring only a single one is shown (Fig. 2). Of the female offspring 9 (Figs. 3–11) are seen to be *hippocoon* like the parent (Fig. 1), while 8 (Figs. 12–19) are the remarkable form *dionysus*, well known but never common all along the tropical West Coast of Africa. *Dionysus* exhibits a strange combination of the patterns of certain mimetic females of *dardanus* with features that are ancestral or reversionary. It is itself non-mimetic, for the one rare Danaine (*Amauris fenestrata*) which is something like it is only recorded from the French Congo. And just as Dr. Carpenter found that the mimetic forms varied away from their models and ran into each other in the islands where the models were few, so this single form, without a model, varies in the localities where its sister-forms, with their models, keep relatively constant. *Dionysus* has never been bred until Mr. Lamborn reared the butterflies here represented, and proved that this relationship holds even within the limits of the same family. It is highly probable that the proportions are Mendelian and the result of a recessive female parent mating with a heterozygote male, and that all the *hippocoon* offspring are recessive and all the *dionysus* heterozygote, but this does not explain the variability of the latter. Mr. C. F. M. Swynnerton has bred families in S.E. Rhodesia which, on the same grounds ‡, are probably made up of recessives and heterozygotes, but in all of these except one all the female forms are mimetic and constant. The single family which forms the exception includes like Dr. Lamborn's a variable non-mimetic female form and a constant mimetic one.

The ancestral part of the pattern of *dionysus* is seen in the fore wing, and the eight specimens have been arranged in the plate to exhibit the gradual transition from Fig. 12 with its fore wing resembling a *hippocoon* (Figs. 3–11) with the triangular white patch of an unusually large size, to Fig. 19 with its fore wing resembling the non-mimetic male (Fig. 2), and still more closely the non-mimetic females of the Madagascar *P. meriones*. It is noteworthy that the triangular fore-wing patch shown in Fig. 12 is more dyslegnic than in any *hippocoon*, although *hippocoon* itself contrasts strongly with the eulegnic model *Amauris niavius*. From Fig. 12 onwards towards Fig. 19 the amount of dyslegnia increases until the bar itself has gone, being represented only by a dusting of dark scales, of which a trace can still be detected in Fig. 19.

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* *I. Congr. Internat. d'Ent.* 1910, vol. ii. p. 483; also *Proc. Ent. Soc. Lond.*, 1911, pp. xci–xcv.

† *Proc. Ent. Soc. Lond.*, 1914, pp. lxiii–lxvi. See also pp. lxvii–lxxi; also *Bedrock*, Apr. 1914, pp. 36, 37, 39. When this latter article was written the whole family had not been received, so that the number of *hippocoon* is given as 6 instead of 9.

‡ See *Proc. Ent. Soc. Lond.*, 1914, pp. lxviii–lxx; see also pp. lvi–lxiii.

The results obtained by Dr. Lamborn, and here represented in the plate, taken in conjunction with Dr. Carpenter's researches in the N.W. Victoria Nyanza and Mr. C. F. M. Swynnerton's in S.E. Rhodesia, offer very strong evidence that the constancy of the mimetic forms which have been the subjects of investigation is due to the operation of natural selection in the presence of the appropriate models, and that when such models are scarce or absent the constancy is no longer maintained on the same level. It is furthermore important that Dr. Carpenter has observed that variations such as those shown in the oblique fore-wing bar of *dionysus* are quite conspicuous on the wing *; and if they are such as to constitute departures from the pattern of the model, there is no reason for believing that the difference is less evident to the eyes of their natural enemies.

G. THE BEGINNING OF MIMICRY: THE FIRST STEP.

Alluding to the resemblance of Chalcosiine moths of the genera *Amesia* and *Callamesia* to the dark blue-shot Euplœas of India, &c., I wrote in 1890 †:—"There are also examples which show us the origin of mimicry—examples in which the resemblance is very imperfect, but, nevertheless, sufficient to afford some protection. . . . . It is extremely probable that the wonderfully close likeness of many mimetic species arose by gradual stages from a general resemblance to a type of colour or pattern possessed by a large group of unpalatable insects." In 1912 I discussed ‡ the origin of the mimetic Uganda female of *Acræa alciope*, which resembles the male of *Planema macarista* and the male and female of *P. poggei*. I gave reasons for the belief that the resemblance to these Uganda models was started by the sudden appearance of a white bar crossing the hind wing. It was also shown that variations of this kind do arise; for out of 294 S. Nigerian females bred by Mr. W. A. Lamborn, a single one exhibited a well-marked white bar crossing the fore wing, thus showing "how a mimetic modification might arise if an appropriate model existed in the locality." The origin of the Uganda mimic was suggested in these words * ;—" It is probable that by spontaneous variation a white band .... appeared in the ancestral form .... and that this was from the very first sufficient to confer some advantage by suggesting the appearance of a dominant Model. .... From this point Natural Selection acting on further variations produced the detailed likeness which we see in the white band itself and in the other mimetic features." After these words were written the opportunity was afforded me of studying Mr. S. A. Neave's collection of butterflies from the Semliki Valley the W. boundary of Uganda, and the forest patches near it. " In his whole collection from this part of Uganda there is not a single mimetic female *alciope* of the eastern [viz. E. Uganda] type: there are many females of the western type, and of these a considerable proportion bear the incipient bar developed to a very variable extent, and sometimes appearing on the under surface alone. Here, then, in the very zone of country where, on the theory of mimicry, we should expect them to be, we meet with the earliest stage of the eastern mimic, but, so far as we know, never the finished product " †.

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* *Bedrock*, Oct. 1913, pp. 360, 361; Apr. 1914, pp. 34, 35.

† *Nature*, Oct. 2. · Reprinted in "Essays on Evolution," Oxford, 1908, p. 376.

‡ *Bedrock*, April 1912, p. 48; quoted in *Bedrock*, Oct. 1913, pp. 301, 302, which should also be consulted, together with the No. for Apr. 1914, p. 45.

The results cannot be explained by climate or any other of the physico-chemical influences of a locality, for the ancestral stage persists into E. Uganda although it is very rare as compared with the fully-developed mimic ‡.

I conclude this section with the following general statement made nearly three years ago § :—" I have always recognised that the first variation must be something appreciable, something which, at any rate, at a distance and on the wing would recall the pattern of the model. Mimicry is far more characteristic of forest species than of those living in the open, and Mr. C. F. M. Swynnerton has made the reasonable suggestion that the origin of mimicry is facilitated by the alternating light and shade of a tropical forest, where it is easy to confuse patterns readily distinguishable under ordinary conditions of illumination " ‖.

I wish to emphasise these earlier statements because, as will appear in the next section, my position has recently been misunderstood.

a. *The Beginning of Mimicry in the North American Nymphaline Butterfly*, Limenitis archippus.—One of the most beautiful and elaborate examples of butterfly mimicry in the world is found in a North American " White Admiral " (*Limenitis*) whose pattern has been profoundly modified in mimicry of invading Danaines. The mimetic pattern has been analysed * by the present writer, who has compared its elements with those of the commonest non-mimetic N. American *Limenitis*. The general results of the comparison are briefly stated below:—

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* *Bedrock*, Apr. 1912, p. 63.

† *Bedrock*, Oct. 1913, p. 303.

‡ *Bedrock*, Apr. 1914, pp. 35, 36.

§ *Bedrock*, Oct. 1913, p. 301.

‖ For the special development of mimicry in forest areas, see *Proc. Ent. Soc. Lond.*, 1912, pp. l–liii.

"The difference between the pattern of the mimic [*Limenitis archippus*] and that of its non-mimetic parent [*L. arthemis*] is enormous – probably as great as that between any two butterflies in the world; but the steps by which the transition was effected were long ago suggested by S. H. Scudder . . . . " †.

"A careful comparison between *arthemis* and *archippus* reveals the most conclusive evidence of selection. The one species has become changed into the other precisely as if an artist were to paint the pattern of *archippus* upon the wings of *arthemis*, retaining unchanged every minute part of the old markings that could be worked into the new, and obliterating all the rest. Thus, extending in this direction and wiping out in that, the great transformation has been effected and one of the most beautiful mimics in the world produced" ‡.

Professor J. F. Abbott has recently criticised § these conclusions or rather his own inference from them—an inference which I am very far from accepting. Professor Abbott takes as his basis the following statement of the selectionist principle as applied to these superficial resemblances:—"In mimicry the selecting influence of the model, if we may use such a term, will be constantly operative upon all individuals of the mimicking species wherever the two are associated in the same habitat" (p. 208). These words are an overstatement, for the selectionist does not claim an influence upon every individual. Exceptional failures in the mimetic likeness may and do survive even when the model is abundant ‖. But it is the following inference from the statement which is especially open to criticism—"it would seem probable therefore, in the case under discussion, that in the districts where *Anosia* [the model] and *L. arthemis* [the hypothetical non-mimetic ancestor of the mimic] occur together, the latter would constantly show in some way the influence of the selective factor. Even if no incipient *L. archippus* is to be found, an aggregate of individuals of *arthemis* ought to show a tendency in that direction by virtue of the fact that by hypothesis the *surviving* adults would be those whose resemblance to the immune *Anosia* has been the means of their preservation from destruction" (p. 208).

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* *Trans. Ent. Soc. Lond.*, 1908, pp. 447–488.

Ann. Ent. Soc. America, ii. 1909, pp. 203–242. Also published in "Darwin and the Origin," London, 1909, pp. 144–212.

Proc. Acad. Nat. Sci. Philad., Jan. 1914, pp. 161–194: issued Apr. 21, 1914.

† "Darwin and the Origin," p. 165.

‡ "Darwin and the Origin." pp 165, 166.

§ "Mimicry in the genus Limenitis with especial reference to the 'Poulton hypothesis,'" *Washington Univ. Studies*, vol. i. Pt. I, no. 2, Jan. 1914, pp. 203–221.

‖ Numerous instances might be given. One of the best has been already described in the non-mimetic *dionysus* form of *P. dardanus* on the W. Coast of Africa (see pp. 43, 44). No doubt "the selecting influence of the model" keeps the mimetic female forms of *dardanus* common, while the absence of a model keeps *dionysus* rare, but it does not prevent the existence of this latter form or of the very rare non-mimetic *leighi* form in Natal.

I regard this inference as quite unsound. I do not believe that the presence of the Danaine model, *plexippus*, has the slightest effect upon the pattern of *Limenitis arthemis*. A colour variation sufficient to cause the one butterfly to be mistaken for the other at any rate under certain circumstances of movement, or distance, or light and shade, &c., must have preceded the evolution of the mimetic pattern as we now see it. If I had thought it possible that such an inference would have been drawn, the present statement would have found a place in the original paper.

Professor Abbott furthermore infers that I committed myself to the belief that the evolution of various elements in the mimetic pattern was simultaneous * (p. 215). I did not intend to express any such belief: I do not hold it. The 1908 paper criticised by him was concerned with an analysis of the fully-formed mimetic pattern of *L. archippus* and the identification of the modified ancestral elements in it—not, except in the most general way, with the sequence or simultaneity of their evolution. I regarded this as a far more speculative matter, perhaps incapable of solution, at any rate not the subject in hand.

Professor Abbott's measurements of colour elements in the pattern of *Limenitis arthemis*, interesting and valuable as they are in themselves, do not affect my conclusions. He finds no evidence of "selection with reference to the mimetic colours" (p. 220) of this non-mimetic species, and I should expect none. I admit that Scudder's statement † quoted by Professor Abbott (p. 204, n. 3) does suggest that the mimicry started in small variations of the orange or red elements in the pattern, but even here there is no suggestion of simultaneous evolution in the other elements. I freely admit too that my own statement ‡ was open to Professor Abbott's interpretation as regards the reddish elements, and these alone,—the very elements which he finds to be specially variable. But, as I have said, it was not my object to attempt, nor did I attempt, to suggest the evolutionary stages in their order, nor the pattern of the hypothetical variety which started the mimetic pattern.

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* Note also the following passage on pp. 217, 218:—"On the basis of Professor Poulton's hypothesis we should expect not only that a selective influence should be evident both in the reduction of the white band and the extension of the red patch, but also that the majority of the surviving individuals [of *arthemis*] should combine these effects."

† "Individuals among the normal species vary somewhat in this particular, so that it is easy to suppose that some of the original *archippus* with more orange than usual may have escaped capture on occasion from this cause. From such a small beginning such as one may now see every year in *B. astyanax* sprang doubtless the whole story...." Scudder's statement seems to me to imply that the reddish elements enlarged first while the other changes followed later. I admit that I have never seen an *astyanax* with the reddish tint so extended as to suggest a probable first step towards the mimetic likeness, but my experience is of course very small compared with Scudder's.

‡ "The character in *arthemis* which initiated the mimicry of *Anosia* is the submarginal row of reddish spots, commonly found in the hind wing, more rarely in the fore" (1908 paper, p. 456).

Now that the question has been raised I am quite ready to express my opinion for what it is worth on so speculative a subject. I believe that the evolution of the mimetic pattern could not have begun upon the upper surface until the appearance of a variety in which a reddish or orange tint had largely replaced the dark ground-colour, and could not have begun upon the lower until a similar or paler tint had replaced the dark chocolate-brown. The wide range of variation in the reddish elements of the pattern referred to by Scudder and proved to exist by Professor Abbott's measurements requires to be greatly extended before the mimetic pattern could begin to arise; but, after that, the pattern was gradually elaborated by the selection of small variations. I believe that the hypothetical ancestor was a butterfly which, as it sailed after the manner of a *Limenitis*, appeared to be of an orange or reddish colour with a broad white band crossing both wings. From this foundation I believe selection has gradually built up the detailed likeness which we see in *obsoleta* and still more perfected in *archippus*.

Professor Abbott has shown by measurements of many individuals that in *arthemis* the white band is a very stable structure (p. 218), as indeed I should have expected from its long persistence in *Limenitis obsoleta* with its beautifully mimetic pattern. The comparison of the Danaine-mimicking North American forms of *Limenitis* with *L. astyanax*, which, although a very close ally of *arthemis*, is without the white band, strongly suggests that it has been a much easier task to get rid of this feature altogether than to mould it in the fore wing into the likeness of the model. Evidence that it is most persistent and has nevertheless been so moulded is afforded by the vestiges which still cling in out of the way places to the mimetic pattern but do not contribute to it, which indeed even slightly diminish the likeness to the model. A feature of especial interest in this respect is the distinct trace of the lower (inner marginal) end of the white band on the fore wing of *L. obsoleta*.

H. MIMICRY BETWEEN THE DIFFERENT INSECT ORDERS.

The inadequacy of the hypothesis that mimetic resemblance arose at a single bound can be shown by innumerable instances of such likenesses between insects of different orders. I will speak of only a single example, and choose it from among "the species of *Scaphura* (a genus of Crickets) in South America [which] resemble in a wonderful manner different Sand Wasps of large size" *, because they are mentioned in Bates' historic

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* H. W. Bates in *Trans. Linn. Soc.*, xxiii. 1862, p. 509. *Scaphura* is now placed among the *Locustidæ* (*Phasgonuridæ*) and not in the *Achetidæ*.

memoir and also because I have recently had the opportunity of studying the details of the mimetic likeness *. The antennæ of the Fossorial Wasps, the models, are of moderate length (about one third that of their mimics), rather stout with a peculiarly emphasised annulation, in colour usually black with a yellow tip. The antennæ of the *Locustidæ* are very long, of almost hair-like fineness, the annulation inconspicuous, the colour uniformly dark with no change at the tip. The antenna of *Scaphura* possesses all the *Locustid* characteristics for the distal two thirds of its length. The basal third, however, is thickened to the diameter of the Fossor's antenna: it has a strongly pronounced annulation and its terminal segments are yellow. At a little distance the hair-like two thirds are invisible and all that is seen is the thick yellow-tipped part resembling the entire organ of the model. To these mimetic details must be added a blue-black iridescence of the abdomen, and above all the great modification which has taken place in the movements, involving changes in the nervous and muscular systems; for the Locustid resembles its Fossorial model and departs from its own group in "the very curious habit of flying and running alternately and of running short distances with expanded wings" †.

It is unreasonable to suppose that such a resemblance as this can have been evolved except by successive stages and in the course of a long period of time.

I. CONCLUSION.

It may be considered that it was unnecessary to devote my last Presidential address to the attempt to prove that small variations are inherited and that mimicry once started has been evolved by the accumulation of small hereditary variations. I have done so because the subjects happen to be those at which I have worked for many years, but also because the views I have attempted to controvert are typical of a restless spirit which, without any real knowledge or serious investigation, seeks to overturn and to destroy. Destructive criticism based on research is a very different thing from an offhand attempt to call in question.

To throw doubt on the germinal origin and hereditary nature of the differences which distinguish geographical races, and thus on the reality of the races themselves, is merely a manifestation of that gratuitous and unnecessary disturbance which, especially in this country, has accompanied much interesting and excellent work at the present day. Although sufficiently disconcerting to those students of geographical biology who take these hasty and unfounded conclusions too seriously, it is however but a slight effort of the "spirit that denies", as compared with the outbreak at Melbourne in 1914 when naturalists were invited to contemplate the whole process of organic evolution as a procedure from the infinitely complex to what by comparison is absurdly simple,—from a Protozoon which contained within it the material germs of all that has been and all that might have been, and, added to these, first the controlling mechanisms which prevented such germs from developing, and then, implied in the last, some mechanism determining the order of their release—from all this to man himself, a mere jack-in-the-box, or rather a combination of jack-in-the-boxes, which, before their lids sprang open, were handed down through the ages.—just one bundle made up out of the infinite variety of finished goods that poured forth, all securely packed, from that illimitable warehouse—the unicellular ancestor! Assuredly he who would suggest this will, in his own words, "be wise to base his faith frankly on the impregnable rock of superstition" *.

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* *Proc. Ent. Soc. Lond.*, 1913, pp. l–liii.

† On the evidence of Dr. Adalbert Seitz, who has often seen model and mimic flying in the same locality near Santos, Brazil. *Proc. Ent. Soc. Lond.*, 1913, p. li.

And now that my term of office has come to an end I wish to express my gratitude to my brother officers and to the members of Councils and of the Society who have made my task so easy and so pleasant—to the Treasurer, the Botanical Secretary and the General Secretary, who had long been in office when I was first elected and have been my kind and sympathetic colleagues and friends for four years. I desire to thank Professor Bourne who gave me kind help as Zoological Secretary until he was obliged to resign in answer to his country's call. We mourn and zoological science mourns the loss of Dr. Assheton who would have been his successor, and of Professor Minchin who held the post for a few short months. And finally I wish to thank my kind friend Mr. Goodrich the present Zoological Secretary who happily will continue to give his help to my distinguished successor.

And here I would speak in few words of Raphael Meldola, not a Fellow of our Society but with us in spirit and one of the band of friends—Darwin, Wallace, Bates, Fritz Müller, and Trimen—who have revolutionised, and largely by means of the Linnean Society, the sciences that are grouped together under the general term Natural History. [And as I am revising the manuscript of this address for publication the last survivor Roland Trimen has passed from among us, so that in under three years we have lost two out of the three authors whose great monographs, published in our Transactions about fifty years ago, laid the foundations of the study of Mimicry in insects.]

How different would have been the feelings with which you would have attended this meeting and with which I should have addressed you, if the happy conditions of the first half of my term of office had been prolonged to the end. But this was not to be; and my debt is all the deeper for the helpful and kindly sympathy which we have received. But I do not wish to dwell

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* *Report British Association*, 1914, p. 11.

on personal and private sorrow as a thing apart. The times call for a wider outlook.

Before the greatest calamity of all time has finally passed away well-nigh every home throughout the land will have known its own pride and its own grief, felt and endured with no bitterness of isolation nor recoil from the intermeddling of strangers, but in fullness of understanding and sympathy made one with national pride and grief.

A nation, and not one nation only but a federation of many nations, thus knit together, will provide a sure foundation for the fearless social and political reconstruction that must inevitably come. In this noble work Science will take a far larger share than she has had in the past, and I am happy in the knowledge that this great Society, under the guidance of my successor and of those who come after him, will hear the inspiring call and give a splendid answer.

APPENDIX.

The Pattern Edges in Pairs of Heliconine Forms. Each pair consists of model and mimic belonging to different Sections. The model apparently belongs more often to Section II.

Heliconius. Sect. II. Opisorhypari.	*Heliconius.* Sect. I. Opisogymni.	Comparison of pattern edges.
H. egeria egerides. Much rarer.	*H. melpomene funebris cybele.*	Both dyslegnic. *Cybele* slightly but distinctly less so in yellow of F.W. and red of H.W.
H. burneyi huebneri.	*H. melpomene thelxiope.* Commoner.	Nearly same. Yellow of F.W. rather more eulegnic, "nail-head" radii of H.W. rather more dyslegnic, all red of H.W. under side much more dyslegnic in *thelxiope*.
H. hewitsoni. Not common; occurs higher but probably overlaps.	*H. pachinus.* Very common but extremely local.	All yellow rather dyslegnic, a little more so in F.W. especially apical marking.
H. sappho primularis. Commoner.	*H. cydno alithea.*	Chief yellow patch of F.W. more eulegnic in *primularis*: H.W. yellow margin less so than in *alithea* and, being much broader than in *sappho elevchia*, recent change is probable as compared with *alithea* whose H.W. margin is same width as *cydno epicydnides*.
H. sappho eleuchia. Commoner.	*H. cydno epicydnides.*	F.W. main patch rather more dyslegnic, H.W. margin rather less so in *epicydnides*.
H. sappho leuce. Commoner.	*H. cydno zelinde.*	*Zelinde* distinctly more dyslegnic.
H. himera. Probably commoner.	*H. melpomene timareta contiguus.*	F.W. rather, H.W. distinctly more dyslegnic in *contiguus*.

Heliconius. Sect. II. Opisorhypari.	*Heliconius.* Sect. I. Opisogymni.	Comparison of pattern edges.
H. microclea.	*H. xenoclea.* Commoner.	Both eulegnic. *Xenoclea* rather less so at basal edge of central F.W. patch.
H. microclea notabilis.	*H. melpomene xenoclea plesseni corona.* Apparently commoner.	*Corona* more dyslegnic with far more scattered red scales in F.W. Red scales in white F.W. patch denser in *notabilis.*
H. erato rothschildi. Very few known.	*H. melpomene aglaope.* Fairly common.	F.W. dyslegnic in both: "nail-head" pattern of H.W. in *aglaope* far more dyslegnic.
H. hydara chestertoni. Much commoner.	*H. weymeri gustavi.* True ab. *gustavi* quite rare, but *weymeri* still scarce, probably because it occurs much higher.	Yellow H.W. bar, the only marking, dyslegnic in both, but more so in *chestertoni.*
H. hydara columbina. Much commoner.	*H. amaryllis rosina.*	F.W. red much more eulegnic in *columbina*: H.W. yellow more so in *rosina.*
H. erato phyllis. Certainly commoner.	*H. melpomene amandus.*	H.W. yellow equally eulegnic. F.W. red far more so in *phyllis.*
No species taken by Burchell (pp. 33, 34).	*H. nanna burchelli.*	Dyslegnic red patch in F.W.: eulegnic yellow bar in H.W.
H. erato phyllis. Very much commoner (pp. 33, 34).	*H. nanna nanna.*	H.W. yellow equally eulegnic: F.W. red far more so in *phyllis.*
H. erato anacreon ottonis. Rare.	*H. melpomene penelope margarita.* Rather uncommon.	Curious fusion of different patterns, very suffused and dyslegnic in both. The large yellow F.W. patch of *margarita* more eulegnic, with appearance of having replaced a eulegnic red patch of which traces remain externally.

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From BEDROCK, Vol. II., No. 3, October, 1913, *pp.* 295—312.

MIMICRY AND THE INHERITANCE OF SMALL VARIATIONS

By Professor E. B. Poulton, F.R.S.

THE inheritance of small variations is an issue of such supreme importance that it would perhaps be well to devote the whole of the present article to its consideration. I will, at any rate, put it in the forefront, beginning by the quotation of two passages in which Darwin summed up the labour and the thought of half a lifetime.

> "Any variation which is not inherited is unimportant for us. But the number and diversity of inheritable deviations of structure, both those of slight and those of considerable physiological importance, is endless. . . . No breeder doubts how strong is the tendency to inheritance: like produces like is his fundamental belief: doubts have been thrown on this principle by theoretical writers alone. . . . If strange and rare deviations of structure are truly inherited, less strange and commoner deviations may be freely admitted to be inheritable. Perhaps the correct way of viewing the whole subject, would be, to look at the inheritance of every character whatever as the rule, and non-inheritance as the anomaly."*
>
> "When a new character arises, whatever its nature may be, it generally tends to be inherited, at least in a temporary and sometimes in a most persistent manner. What can be more wonderful than that some trifling peculiarity, not primordially attached to the species, should be transmitted. . . .
>
> "Some writers, who have not attended to natural history, have attempted to show that the force of inheritance has been much exaggerated. The breeders of animals would smile at such simplicity, . . ."†

Why should Professor Bateson, Professor Punnett and their followers make assertions which imply that Darwin was a hasty generaliser, that his opinions on fundamental questions were ill-considered and of no importance ? The answer is a simple one. These clever and ingenious men, dazzled and confused by a rediscovery of the utmost interest, and the exciting investigations to which it has led, have entirely lost all perspective and all sense of proportion. Their distorted vision is most unfortunate for English biological science, because young and vigorous naturalists, ever eager in the pursuit of some new thing, are being led into the same hopeless confusion which has overwhelmed their leaders. It is well that the danger should be seen and guarded against, that men should know how far these writers are to be taken seriously when they wander, as they are so apt to do, beyond the details of their own researches. The irresponsibility of de Vries's principal exponent in this country is manifest in the following passages quoted from the same volume* and only eleven pages apart :—

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* *Origin of Species*, 1st. ed., 1859, pp. 12, 13.

† *Variation of Animals and Plants under Domestication*, Vol. I., 1875, p. 446. The same conclusion is re-stated and examples given on pp. 447 and 449.

De Vries according to Bateson.	*De Vries according to De Vries.*
" First we must, as de Vries has shown, distinguish real, genetic variation from *fluctuational* variations, due to environmental and other accidents, which cannot be transmitted " (p. 95).	" Thus we see that the theory of the origin of species by means of natural selection is quite independent of the question, how the variations to be selected arise. They may arise slowly, from simple variations, or suddenly, by mutations ; in both cases natural selection will take hold of them, will multiply them if they are beneficial, and in the course of time accumulate them, so as to produce that great diversity of organic life, which we so highly admire " (pp. 83, 84).

An even sharper contrast is evident between the following passages from the same authors. First, Professor Bateson :—

> " For the first time he [de Vries] pointed out the clear distinction between the impermanent and non-transmissible variations which he speaks of as *fluctuations*, and the permanent and transmissible variations which he calls *mutations*."†

Now Professor de Vries himself :—

> " Sugar beets afford the finest example of the process of artificial

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* *Darwin and Modern Science*, Cambridge, 1909.

† Mendel's *Principles of Heredity*, Cambridge, 1909, p. 287.

> selection. In no other plant under cultivation has the technique of selection reached so high a pitch of perfection ; in no other is the method so sure or the result so certain. There is now no sale for beet seed which has not been the result of careful selection.
>
> " Experiments in the selection of sugar capacity began about 1850. This instance shows best, therefore, what can be achieved within half a century by continued selection in one and the same direction, hand in hand with continual improvement of method.
>
> " Progress has been enormous : the average content of the common beet, which at first was a matter of 7—8 %, is now double that amount. Shape, size, and weight, the character of the leaves and especially the reduction in woody tissues have all been the object of selection, and have made the beet much more valuable from the industrial point of view.
>
> " All this has been done by selection of the best individuals afforded by ordinary fluctuating variation. Neither spontaneous variations nor crossings have played any part in it. We are dealing here with the process in its simplest form."*

It is surely the irony of fate that I, who, admiring de Vries as an investigator, think nothing of his contributions to the evolution theory, regarding them as in part already to be found in Darwin and Galton and, when original, puerile—that I should have to correct his professed supporters and exponents, and explain the meaning of a de Vriesian " fluctuation " as contrasted with his " mutation." The difference is *not* that the first are non-transmissible and the second hereditary, but that fluctuations are liable to regression and more and more liable to it the further they have been advanced in any direction by means of selection. Mutations, on the other hand, are a leap to a new position of genetic stability. In all these conceptions de Vries is merely following Galton, who earlier expressed the same conclusions far more clearly and with a much better terminology. I must add that a perfectly correct account of de Vries' conclusions has been given by A. A. W. Hubrecht,† C. B. Davenport,‡ R. H. Lock§ and J. Arthur Thomson.‖

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* *Die Mutationstheorie*, English Translation by Farmer and Darbishire, Vol. I., 1910, pp. 99, 100.

† *Popular Science Monthly*, July, 1904, p. 205; *Contemporary Review*, No. V., 1908.

‡ *Fifty Years of Darwinism*, New York, 1909, pp. 173—4.

§ *Variation, Heredity and Evolution*, 2nd ed., London, 1909, pp. 75, 135—6, 155.

‖ *Heredity*, London, 1908, pp. 78, 98. Quotations from all these writers, In spite of de Vries himself, in spite of all that the above-named writers have said, a "de Vriesian mutation," which is the same thing as Galton's better-named "transilient variation," is rapidly being replaced by a "Batesonian mutation," which is the same thing as Weismann's better-named "blastogenic variation"—also called by various writers at various times *constitutional*, *congenital*, *centrifugal*, *genetic*, *inborn*, *innate* and *inherent*. It is a formidable list, and the only objections to adding mutation to it are that it is the least descriptive, the most recently applied, and, because of its history, by far the most confusing term of a list that is already quite long enough.

Mighty is the force of fashion, in science as in other departments of human activity. Even my friend the Master of Christ's College, Cambridge, who very nearly a quarter of a century ago laboured with Dr. Schönland and with me to make known Weismann's conclusions on heredity, even he now hands over to de Vries what de Vries himself has never claimed, viz., Weismann's clear distinction between blastogenic and somatogenic characters.* So also Clifford Dobell, in a passage with a wording which goes far to suggest Weismann's term blastogenic, prefers to perpetuate this cause of confusion, error, and injustice :—

> "By *mutation* . . . I mean a permanent change—however small it may be—which takes place in a bacterium and is then transmitted to subsequent generations. The word does not imply anything concerning the magnitude of the change, its suddenness, or the manner of its acquisition. The term denotes a change in genetic constitution. All other changes which are impermanent —depending generally upon changes of the environment—and not hereditarily fixed, are called *modifications*."†

The word mutation—originally introduced by Waagen, used in a different sense by de Vries, used in a third sense erroneously ascribed to de Vries by Bateson—is bringing "confusion worse confounded" upon biological thought. In the interests of clear thinking I cannot help regretting this unnecessary result, although the spread of the word in the Batesonian sense places me in the

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as well as a fuller discussion of the unfortunate confusion into which the subject has been thrown, will be found in the author's *Darwin and the Origin*, London, 1909, pp. xi.—xiii., 48—51, 258—280.

* Presidential address to Section D. at Winnipeg, 1909.

† *Journ. Genetics*, Vol. II., No. 4, p. 326.

happy position of the prophet who sees fulfilment even earlier than he expected.

> "A humorist has suggested that the Homer controversy should be settled by a general agreement that the *Iliad* was written not by Homer but by another man with the same name. Those who have heralded with such a flourish of trumpets the profound changes which they assume to be necessary in the Darwinian conception of evolution, may yet save their face by calling the same thing by another name."*

I now come to details of Professor Punnett's article in the July number of BEDROCK, and I here find the irresponsibility already spoken of, the same attitude which seems to be expressed by the words—"Mendelism is so interesting that it really doesn't matter what one says." Thus, on page 153, speaking of the inheritance of a small variation, we are told that "in no clear case has it been shown to exist." Does Professor Punnett believe that "family likeness" is hereditary, or that one element in family likeness, such as the shape of a nose or chin, is hereditary; that a voice or trick of movement or expression is hereditary? I do not think that he doubts any of these facts. His statement was just the irresponsible utterance of one who has not thought out the consequences of his own words. And if Professor Punnett still has doubts, at any rate they are not shared by others who are as interested in Mendelian research as he is himself. Thus Professor C. B. Davenport told me in 1909 that he had often been struck with the remarkable persistence of insignificant variations, such as a single small white spot. But leaving the higher animals and coming to butterflies, I had spoken, in the very article † supposed to be criticised by Professor Punnett, of actual evidence in the Hope Collections that "small features in the pattern of the parent [*dardanus*] certainly tend to reappear in her offspring," and one such feature was described. Professor Punnett never even alludes to the passage. Nor does he refer to Figs. 11 to 14 in Plate III. of my article, distinctly proving that a small variation in pattern exhibited in the female parent was inherited by all her offspring of the same form (*dubia*). I also mentioned on p. 56 that Mr. Lamborn had sent me another much larger family showing the same hereditary persistence of the same small variation. Of course, it is possible to argue at some length as to what is "small" and what "large," and I will therefore endeavour to avoid all unnecessary discussion by explaining that the "small" variation, described on p. 56 and shown to be hereditary in Plate III., is just such a change as, in my opinion, formed one of the steps by which a mimetic resemblance was attained. Mr. Lamborn also sent to me, in the early part of last year, two magnificent families of *Hypolimnas dinarcha*, together with their female parents. In one parent the white of the hind wing is faintly tinged with yellow, and there is a very slight difference in the pattern of the fore wing. Both these characteristics, as small or smaller than the "steps" I have postulated, strongly tend to be inherited by the female offspring.

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* *Darwin and the Origin*, p. 280.

† BEDROCK, April, 1913, p. 50.

It is, furthermore, easy, by a study of the geographical races of almost any wide-ranging species, to supply the evidence Professor Punnett has failed or not troubled to find. The fine work of the Tring Zoological Museum is chiefly devoted to the comparison, description and illustration of these small hereditary differences between races which, by inter-breeding at the margins of their respective areas, are welded together into a single species. I will illustrate this kind of evidence, of which any amount is available, by reference to one of the species mentioned and figured on Plate I., facing p. 151 of Professor Punnett's paper. The figures of *Danais chrysippus* clearly show the pattern at the tip of the fore wing of average Indian and Cingalese examples. A small white spot is seen lying opposite the lower end of the white bar on the side turned towards the attachment of the wing. This spot, if it were larger and joined to the bar, would make with it an L-shaped marking. When we follow *D. chrysippus* eastward, for example, into the Macao and Hong Kong districts, that spot does become larger and is sometimes joined to the bar. Following the butterfly westward into Africa, the spot disappears altogether, or, when it persists, is smaller than in Professor Punnett's figures. Other minute geographical changes in the same butterfly might be described, and, as I have said, any number in other species. The only question that remains is their transmissibility, but I imagine that Professor Punnett will hardly doubt that each local pattern of a butterfly, occupying corresponding stations in the different parts of its total habitat, is a hereditary pattern. There is really no room for doubt, because geographical races, including some forms of *chrysippus*, have often been bred and found to come true.

Professor Punnett—unintentionally no doubt—misinterprets my views as to the first origin of a mimetic likeness in a butterfly with a pattern widely different from its model. More than once he speaks of the "minute initial variation," or words to that effect: on p. 153 he alludes to "the difficulty of the initial stages, so clearly recognised by Darwin, and so lightly disposed of by" me: on p. 146 he refers to an interpretation based on the theory of mimicry as "altogether too facile." I am sorry to indulge in a *tu quoque*, but I must point out that it is very easy to meet the difficulty of the origin of a mimetic likeness by assuming that it appeared in its present form. I have never found it light and simple work to attempt to make out these past histories. The careful study of a long series of specimens from many parts of as wide a range as possible is generally required, and after doing one's best the dominant feeling at the end is often the desire for more specimens from other localities. If Professor Punnett had troubled to study what I have written he would never have spoken as he does about the supposed "minute initial variation." I have always recognised that the first variation must be something appreciable, something which, at any rate, at a distance and on the wing would recall the pattern of the model. Mimicry is far more characteristic of forest species than of those living in the open, and Mr. C. F. M. Swynnerton has made the reasonable suggestion that the origin of mimicry is facilitated by the alternating light and shade of a tropical forest, where it is easy to confuse patterns readily distinguishable under ordinary conditions of illumination.

In an earlier article in BEDROCK* I attempted to trace the origin and history of the mimetic pattern of the eastern female of *Acraea alciope*, which resembles the male of one species of *Planema* and the male and female of another. I gave reasons for the belief that the eastern mimicry was started by the sudden appearance of a white bar crossing the hind wing. I furthermore showed that out of 249 western females bred by Mr. W. A. Lamborn in the Lagos district, a single one exhibited "a well-marked white bar crossing the fore wing," showing "how a mimetic modification might arise if an appropriate model existed in the locality." Concerning the origin of the eastern mimic, the following passage is quoted from p. 63 :—

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* No. 1, April, 1912, p. 48.

> "It is probable that by spontaneous variation a white band like that shown in Fig. 13 appeared in the ancestral form (Fig. 12), and that this was from the very first sufficient to confer some advantage by suggesting the appearance of a dominant Model (Fig. 6). From this point Natural Selection acting on further variations produced the detailed likeness which we see in the white band itself and in the other mimetic features."

I think Professor Punnett will admit that he has given an unfair impression of my views. But it is not only for the purpose of correcting him that I quote rather fully from the earlier article. In writing it I left off as usual longing for more material. Within the past few months the wish has been gratified. The paper was written after a study of the splendid western series sent to me by my friend, Mr. W. A. Lamborn, Entomologist to the Agricultural Department of Southern Nigeria, and the equally splendid material from Eastern Uganda by my friends, Mr. C. A. Wiggins, D.P.M.O., of the Uganda Protectorate, and Dr. G. D. H. Carpenter, Member of the Royal Society's Sleeping Sickness Commission. The eastern females were nearly all perfect mimics of eastern models, but a very few were of the western type, and of these again a small proportion exhibited the incipient but distinct white bar which suggested the origin of the eastern mimetic form. I was especially anxious for specimens from further west, from a zone of country where I thought the transitional forms might be abundant. Owing to the kindness of my friends Mr. S. A. Neave and Mr. Guy A. K. Marshall, Secretary to the Entomological Research Committee of the Colonial Office, I have now had the chance of studying carefully the fine collection made in Uganda by the former as travelling naturalist to the Committee. Mr. Neave not only collected in Eastern Uganda, with results as regards the female *alciope* similar to those obtained by my other friends, but also travelled westward to the Semliki Valley, the western boundary of Uganda. He here entered the margin of the great tropical forest which stretches unbroken to the west coast. Uganda itself is largely open country with patches of primitive forest, doubtless formerly continuous with one another and with the great forest now ending at the Semliki.

Mr. Neave collected in the Semliki Valley and in forest patches near it. In his whole collection from this part of Uganda there is not a single mimetic female *alciope* of the eastern type: there are many females of the western type, and of these a considerable proportion bear the incipient bar developed to a very variable extent, and sometimes appearing on the under surface alone. Here, then, in the very zone of country where, on the theory of mimicry, we should expect them to be, we meet with the earliest stage of the eastern mimic, but, so far as we know, never the finished product.

I can hardly expect that this evidence will appeal to Professor Punnett, who seems to be singularly impervious to arguments based on geographical distribution. Thus he makes no reference, save one, to the distribution of the mimetic and other forms of *P. dardanus*, although geographical distribution was the strongest part of the argument he was professing to answer. His one reference hardly strengthens his case. He speaks of "wildly assuming that because a form lives on an island it is therefore ancestral" (p. 164). No assumption was made on such grounds. *Papilio meriones* was held to be ancestral, not because it lives in Madagascar, but because the female possesses the non-mimetic pattern of the male. And Professor Punnett, too, when it suits his purpose, is quite willing to base his arguments on the conclusion that the non-mimetic male of a mimetic species bears the ancestral pattern.* Incidentally it may be remarked that it is somewhat humorous for Professor Punnett to speak of anyone wildly assuming anything.

While we are on the subject of *P. dardanus* it will be convenient to correct another mistaken assumption. Professor Punnett begins a paragraph on p. 161: "Let us . . . for the sake of argument, leave out of account the fact that some, at any rate, of these transitional forms (such as *trimeni*) are specific. . . ." *Trimeni*, named by me in 1906,† is not specific, and has never been spoken of as specific by any writer except Professor Punnett in the above-quoted passage. It is a female form existing side by side with other and mimetic female forms in the sub-species *polytrophus* and *tibullus* of *Papilio dardanus*. Plate II. of my last Bedrock article would have shown this clearly to Professor Punnett if he had studied it even superficially ; for seven of the figures are distinctly labelled " *Polytrophus* male " and " 6 *Polytrophus* females of 4 forms," two of the latter being named "*trimeni*." No trouble is necessary in hunting up reference numbers in a description of the figures. All the information is printed on the face of the plate. I think I am entitled to use Professor Punnett's words on p. 161 and ask for "a more critical spirit."

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* See pp. 151, 152, of his BEDROCK paper. It is a pity that in Plate I., facing p. 151, in which Professor Punnett illustrates his argument, *D. chrysippus* should be represented by a male in both outer and inner circles, although all the other species are represented by males in the outer and females in the inner circle.

† *Trans. Ent. Soc., Lond.*, 1906, p. 283.

It is difficult to take seriously Professor Punnett's reply to my criticism* of his statement that, according to the Darwinian view, a certain African Danaine butterfly arose direct but gradually from another, and that, according to the Mendelian, the origin was sudden.† I pointed out that no one had ever suggested such an origin at all, and that those who had studied the group placed the two species rather far apart. Professor Punnett's reply is curious. The conclusions on the zoological affinities of his group reached by the great Swedish naturalist who has spent most of his life in the exact and careful study of African butterflies he likens to those of Moses, his own conclusions on the same question reached by no study at all, he compares to those of the modern zoologist! This is the way in which he is concerned to defend an elementary exposition of his subject intended for the non-scientific public!

Returning for a moment to the female *Acraea alciope*, I think that the facts brought forward in the first number of Bedrock, together with Mr. Neave's more recent discoveries referred to in the present paper (pp. 302, 303), will convince the great majority of naturalists that the mimetic pattern was attained by steps and not suddenly. Yet the result is here far less elaborate than that seen in the two mimetic females of *Papilio polytes* which Professor Punnett maintains were produced at a single bound. I have never yet written on the evolution of these females, and, since the history as I interpret it is different from that which Professor Punnett ascribes, on pp. 153 and 154, to the followers of the theory of mimicry, it is appropriate that I should do so on the present occasion. I have the advantage of writing with several specimens from Ceylon as well as some from other parts of the geographical range beside me—the former collected and kindly given to me by Professor Punnett himself.

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* Bedrock, April, 1913, p. 52.

† *Mendelism*, 1911, pp. 134—5.

Professor Punnett's Plate II., facing p. 153, gives a fair idea of this butterfly and its two models. The reference numbers to the *hector* and *aristolochiæ* forms are unfortunately transposed on p. 153, and on the plate the intense red spots on the hind wings and the same vivid tint on the body of one model, *P. hector*, are invisible, while the dull red spots on the hind wings of the other model, *P. aristolochiæ*, can be detected with difficulty. The photograph required screens, special plates and long exposure to give a good reproduction of these difficult tints, but its failure has a special interest in relation to the present discussion. To the human eye the red of *P. hector* is so aggressively assertive that an æsthete of thirty or forty years ago would have declined to live in the same house with the butterfly; yet, upon Professor Punnett's photographic plate, it produced the same effect as black. The dull unobtrusive red of the corresponding mimetic female would have been tolerated or even welcomed at the period of "Patience"; yet it asserts itself on the plate and comes out in its true value against the black background of the wing. It is evident that the pigments are quite different, and spring from different genetic factors in model and mimic.

Professor Punnett supposes (p. 155) that the two mimetic females arose suddenly in their present form from the male-like female. "After all," he says, "the different females of *polytes* are doing the same sort of thing every day." Men with potential aptitude—more or less—for reasoning are born every day. Does Professor Punnett therefore believe that man as he is now arose suddenly from a common ancestor with the anthropoids? If not, the fact that the different females of *polytes* are produced now is hardly an argument that they were originally produced in their present form. I would ask any thinking naturalist to look at Professor Punnett's Plate II. and compare the two mimetic females (3 and 4) with their two models (5 and 6) and with their non-mimetic ancestor (2), to note carefully the various points of resemblance to the models and of difference from the ancestor—points analysed on pp. 308—10, and then consider whether it is reasonable to suggest that all these features in the pattern—some of them detailed and nearly exact, such as the V-like white marks near the apex of the fore wing in the "*hector* form" (3)—that all these arose suddenly and together in each of the two mimics. That a large variation may arise suddenly no one ever doubted, but not many naturalists will accept the view that a complex pattern of many elements resembling the corresponding elements in an entirely different species could spring into existence as a whole and complete in all its details.

Granting the sudden origin of the two mimetic forms, Professor Punnett admits, on p. 155, that they would be preserved and rendered predominant by Natural Selection, but it is difficult to reconcile this part of his paper with pages 156 to 158, in which he reaches the conclusion that the proportion of the mimetic females in Ceylon expresses a Mendelian equilibrium undisturbed by selection. *Papilio polytes* has a wide range in the Oriental Region. Over most of this range it is accompanied by one model only, and not two; in certain localities this single model is so scarce that it is impossible to believe that it can act as a model at all. With these facts, which enable him to ascertain what actually happens in the absence of one or both models (as effective agents), Professor Punnett light-heartedly chooses Ceylon, where both models are common, as his crucial locality, and, entirely neglecting comparison with other areas, concludes, with all the emphasis of italics, that "*Natural Selection is non-existent in so far as concerns the relation of the mimetic to the non-mimetic females of Papilio polytes*" (p. 158).

Now let us see where the facts lead. *Papilio hector* is only found over a part of the area of *polytes*, and of the second model *aristolochiæ*. Localities in this part, Ceylon being one, yield both forms of mimetic female. Localities in the area outside this part yield one mimetic female, the "*aristolochiæ* form." The species forms an interbreeding community, at any rate over the continental part of its range, and it is to be expected that a certain small proportion of "*hector* females" will stray into the country outside the boundary of their model. I only suggest this probability from an experience of *dardanus* and other mimetic species in Africa. In the Hong Kong and Macao districts *P. hector* is unknown, and so is its mimic: *P. aristolochiæ* is excessively rare, so much so that some observant naturalists long resident in these localities have never seen it at all. *Papilio polytes* is, according to these naturalists, the commonest or one of the two commonest swallow-tails of the locality. Here then is a splendid opportunity for Mendelian equilibrium. What we really find is the almost complete preponderance of the male-like female. I have lately received six females—all of this form—captured by Captain R. A. Craig on Stonecutter's Island, in Hong Kong Harbour. Not a single model was present in the collection. Dr. Seitz, in a long experience of the Kowloon district, never saw any other form of female and never saw the model. Commander J. J. Walker alone thought that the "*aristolochiæ* form" was as common as the non-mimetic form at Hong Kong, although he, too, never saw the model. Mr. J. C. Kershaw's experience at Macao corresponds with that of most observers at Hong Kong. He finds the male-like female of *polytes* is the common one and has never seen *P. aristolochiæ*.* The opposite condition is found in New Guinea, where the representative of *polytes* has but a single female form mimetic of the representative of *P. aristolochiæ* and the male-like form is unknown.

In order to reach safe conclusions we really need many cabinets filled with specimens of this butterfly and its models from localities scattered over representative parts of the range. Many thousands of specimens are required. But we already know enough to feel confident that the two mimicking females only occur regularly where the two models are common, and that when one model is absent and the other common, the corresponding mimetic female is common; finally that when the single model is wanting or extremely rare the corresponding form is absent or rare. The facts do not warrant Professor Punnett's italicised conclusion quoted on p. 306.

I will now attempt to trace the evolution of the two mimetic females of *polytes*. I do not believe for a moment that the species is palatable to insect-eating animals in general. The under-surface pattern of the male closely resembles its upper surface, only differing in that it is rendered even more conspicuous by the larger yellow marginal markings on the hind wing as well as by a row of red spots lying within these markings. Such a relationship between the upper and under surface is also found in *P. aristolochiæ*, and is very characteristic of the groups which supply the best-known models for mimicry. It is the very opposite of the relationship seen in butterflies with a dead-leaf-like or otherwise procryptically-coloured under-surface to the wings. The mimicry is, I hold, Müllerian, and the mimetic forms have merely exchanged the warning patterns peculiar to their kind for those characteristic of two other far more distasteful species with a more flaunting and slower flight. An exchange like this of one conspicuous pattern for another, when it can be established, seems to me a good criterion of Müllerian mimicry. We should expect a Batesian mimic to be developed out of a species with a procryptic under-surface. Professor Punnett accepts without question Haase's hypothesis that the distasteful qualities of the models are derived from the food-plant. Haase may be right, although I have always felt that stronger proof is required, but under any circumstances distasteful qualities can be elaborated in the body and are not necessarily borrowed direct or with slight change from the food-plant. Commander Walker has told me of the larva of the Australian *Papilio macleayanus*, feeding on the "Sassafras tree," *Atherosperma moschatum*, which emits from the well-known pair of glands behind the head a "strong and very disagreeable scent"—which is "totally unlike the pleasant nutmeg-like fragrance of the Sassafras, but resembles that of butyric acid or the smell of the little malodorous ants of the genus *Cremastogaster*."* Commander Walker even found that the caterpillars were more easily collected by smelling for them than by looking for them. A citronaceous food-plant is not evidence of the palatability to insect-eaters of *P. polytes*.

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* See *Proc. Ent. Soc. Lond.*, 1913, pp. xxxi., xxxii., where observations in the Hong Kong and Macao districts are recorded and references given.

We now come to the transformation of the non-mimetic into the mimetic forms. Professor Punnett assumes (pp. 153, 154) that "on the theory of mimicry" the two forms were evolved independently; but I do not think there is the slightest doubt that the mimic with a far wider range, the "*aristolochiæ* form," was evolved first and that later on the "*hector* form" was developed from it and not direct from the male-like female. The essential and first change, upon which the detailed likeness to *P. aristolochiæ* has been built up, was, I do not doubt, the shortening and widening of the yellow bar crossing the hind wing of the female *polytes*. The bar is not only widened by the lengthening of its central constituent spots, but by the appearance of a patch of yellow at the end of the cell. A very similar shortening and widening of a yellow bar crossing the hind wing is to be seen in an African Nymphaline butterfly, *Neptis woodwardi*.* The mimetic transformation is here evidently very recent, and distinct progress is seen† when we pass from the N.E. shores of the Victoria Nyanza to the Kikuyu country, east of the Rift Valley, where the Danaine model (*Amauris albimaculata*) is especially predominant, and other mimics of its pattern abound.‡ Such a change in its most conspicuous element would by itself cause the pattern of *polytes*, upon the wing or at a little distance when at rest, to suggest that of *aristolochiæ*. The remaining features of the resemblance were then gradually added, each contributing something to the effect and suggesting more and more strongly the pattern of *aristolochiæ* : (1) the disappearance of the marginal yellow spots of the fore wing, (2) the emphasis and reproduction, on the upper surface, of the sub-marginal spots of the hind-wing under surface—already present in the male and generally red, although sometimes yellow, already tending to appear on the upper surface of some male-like females ; (3) the peculiar light-and-dark striation of the outer half of the fore wing, and its reproduction with a marked brightening of the pale elements on the under surface ; (4) lastly, the almost entire disappearance from the hind-wing upper surface of the yellow lunules marking the bay-like indentations of the margin—a character already extremely variable in the male and male-like female. I do not mean to imply that these changes took place in the above order or that none of them occurred simultaneously. Comparison with the "*hector* form" renders it probable that (4) was the last change (see p. 310).

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* *Ent. Mo. Mag.*, xli. (1905), p. 220.

Now that the elements in the resemblance to *P. aristolochiæ* have been analysed, the improbability of their all appearing together at the same moment is emphasised. That Mendelian heredity has probably played an important part at some of the stages I freely admit. Why Professor Punnett should prefer to think that the Mendelian principle can only act once in the history of a mimetic form I am at a loss to imagine. Some mimetic transformations are simple, some are excessively complex; he seeks to explain them all by a single variational leap. What reason has he for thinking that variational activity—whatever may be its unknown cause—like certain flowers, can only bloom once? Why should he seek to lay this hard burden on the Mendelian principle as a factor in evolution? This question is raised at the present point by the remarkable contrast between the simple evolution of the "*hector* form" and the complex transformation I have attempted to describe in the preceding pages. As regards the hind wing, the "*hector* form" possesses almost precisely the pattern of the "*aristolochiæ* form" with its yellow transformed into red—a change which may well have occurred suddenly. The comparison between Figs. 3 and 4 on Professor Punnett's Plate II. shows the nature of the transformation, but to appreciate it fully the actual specimens should be studied. The marginal and sub-marginal lunular markings are larger in the "*hector* form," and this is the only constant difference between the hind-wing patterns of the two forms. As regards the marginal lunules it is probable that the "*hector* form" arose before these markings had become evanescent, as they now are on the upper surface of the "*aristolochiæ* form." These markings—although out of place in a mimic of *P. hector*—are red like the rest of the hind-wing pattern in the "*hector* form," a probable indication that the change to red was a single transformation, involving some divergence from the new model, although, upon the whole, resemblance to it. At the same time the likeness is a rough one, for, as I have said, the hind-wing pattern, apart from its colour, is that of the "*aristolochiæ* form" and its model. The fore-wing pattern is doubtless the most conspicuous part of the "*hector* form," and here the likeness to the model is far more convincing. It has obviously been produced from the striated fore wing of the "*aristolochiæ* form" by reducing certain parts and emphasising others, on both surfaces, and, upon the under, distinct traces of the increased paleness of the older form are retained on parts of the wing that are black in the model, *P. hector*.

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* *Trans. Ent. Soc. Lond.*, 1908, p. 512.

† *Ibid.*, Pl. XXIX., Figs. 2 and 4.

‡ *Ibid.*, Pl. XXVIII.

How can we account for the evolution of two mimetic forms in a butterfly which remains dominant when its models are absent or excessively rare ? It is worth while to consider this question in some little detail, for I believe that the true explanation is different from that usually given.

Papilio polytes is an unusually dominant and successful swallowtail. Its rate of reproduction, combined with a probable measure of distastefulness advertised by a conspicuous pattern, its powers of flight, alertness, and other adaptations of many kinds, keep up the large average numbers in spite of the attacks of enemies of all sorts in all the stages of its life-history. The large numbers that survive in every generation will, of course, include the fittest, and so the high level of protective efficiency is maintained. This is the condition of *polytes* in the Hong Kong and Macao districts where the single model is so rare that it is unreasonable to suppose that it exerts any effect, and this was doubtless its condition before the evolution of the mimetic forms. There is no reason to suppose that the surviving percentage of *polytes* was increased by the presence of the *aristolochiæ* model or during the growth of the mimetic likeness. All that happened was this : certain variations formerly unselected, now tend to fall into the surviving percentage, and, once started, the further stages of transformation were effected in the same way. Each change that suggested still more strongly an advertisement common to a far more distasteful form would tend to be selected. So, too, when *polytes* spreads beyond the range of *aristolochiæ,* or when the model for some reason disappears from an area in which *polytes* is abundant, the constitution, not the amount, of the surviving percentage is changed. The mimetic pattern soon disappears, although the species that bore it remains as abundant as before. The survival or extinction of the species is not affected : all that has happened is the survival or extinction of a pattern borne by a certain proportion of the individuals of the species. When these disappear other individuals with another pattern take their place. It is, furthermore, extremely probable that selection is reversed when the models are absent, for a female that resembles the male is better advertised than one which resembles a non-existent model. Although I believe that many mimicking species bear the above-described relationship to their models, I do not mean to imply that this is always so. No doubt there are plenty of mimicking species which depend upon the presence of the model for their existence and could not live in areas from which the model disappeared.

I have answered the main points raised by Professor Punnett, and should have been glad of the opportunity of discussing them all, but it seemed better to devote a considerable part of the present article to *Papilio polytes*, and thus offer what a Darwinian really believes as a substitute for what he is assumed to believe.

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Section D.—Hull, 1922.] [BRITISH ASSOCIATION.
Report, p. 372.

Prof. E. B. POULTON, F.R.S.—*Experimental Evidence for the Hereditary Transmission of Small Variations such as would be required to initiate a Mimetic Resemblance in Butterflies.* (3 p.m.)

The *sudden* evolution of a complex mimetic pattern, fully formed and complete, is difficult or even impossible to explain. We are compelled to believe that there has been a development in stages, each represented by a comparatively small variation. Certain authorities on heredity have maintained that such variations are not transmitted. An investigation designed to test this conclusion has been carried on with the common Currant Moth (*Abraxas grossulariata*), and it has been shown that the fusion of two black patches on the fore wing into a single bar, present in the female parent, was transmitted to nearly all of her offspring. Next year will probably decide whether the transmission followed Mendelian laws; but, Mendelian or non-Mendelian, the variation was certainly hereditary, and was of just such a kind and magnitude as would furnish one of the steps towards a complex mimetic pattern.

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From BEDROCK, No. 1, *April*, 1914, *pp.* 34—45.

THE EVOLUTION OF MIMETIC RESEMBLANCE

By Professor E. B. Poulton, F.R.S.

In my last article in the October number of Bedrock I found it necessary to devote the greater part of the available space to an issue that had been raised by Professor Punnett—the inheritance of small variations. This was an issue so tremendous that the immediate controversy on Mimicry became by comparison insignificant, and I had the less hesitation in cutting it short because I had already written elsewhere on the questions put by Professor Punnett. He now suggests that some of these questions were unanswered in my last article because I had no answer to give. I will, therefore, put his points *seriatim* in the forefront of the present article, summarising under each the answers that have already been given and including new evidence when such is available.

(1) The theory of mimicry "confers upon minute variations a selective value which is inconceivable when regard is had to the nature of the selecting agent." To most naturalists it is not only conceivable, but even certain, that many kinds of birds can see as well as or better than man. I have published some evidence on this subject in the *Proceedings of the Entomological Society of London* (1912, pp. liii—lv). That the sight of man can easily appreciate the "minute variations" alluded to by Professor Punnett is proved by an example published on p. cxxxviii of the same *Proceedings*. The evidence is so interesting that I will quote it in full. Dr. G. D. H. Carpenter wrote to me, September 21st, 1912, from Bugalla, one of the Sesse Islands, in the north-west of the Victoria Nyanza :—

> "I caught a very nice *initial variety* of *Ps. terra* the other day. It had a very slight yellow suffusion of the black ground-colour

> along the costal margin of the forewing, and the black bar between the sub-apical and hind-marginal tawny areas was slightly thinned away. This specimen, however, *looked distinctly different*, both at rest and on the wing, which tends, I think, to show how the smallest variations may have selective value. This is always rather a stumbling block, so it was nice to see it actually exemplified."

Dr. Carpenter alludes to this and other small variations of the same mimetic pattern in this journal for October, 1913 (pp. 360—1),* bringing them forward, in fact, as an answer to this very objection. The butterflies referred to by Dr. Carpenter may be studied by any naturalist in the Oxford University Museum. They are good examples of those " minute variations " which, as I believe, have provided the steps by which mimetic resemblance has been attained.

(2) The theory of mimicry " makes the sweeping assumption that such minute variations are inherited." In answer to this objection I gave, on pp. 299—300, several examples of the inheritance of small variations, most of which are passed over in silence by Professor Punnett. I asked if he believed " that ' family likeness ' is hereditary, or that one element in family likeness, such as the shape of a nose or chin, is hereditary ; that a voice or trick of movement or expression is hereditary ? " I gave examples of such inheritance in mimetic butterflies, described and illustrated in earlier papers, and said that he had never even referred to them. In his latest paper he still neglects them. I shall have more to say about the one example, *Danaida chrysippus*, that he attempts to explain as the result of climatic influence. In the meantime there is one piece of evidence brought forward in my last paper which has so important a bearing on this very question that I venture to refer to it again. I spoke on pp. 302, 303, of the geographical changes in the females of *Acræea alciope*, showing that " in the very zone of country where, on the theory of mimicry, we should expect them to be, we meet with the earliest stage of the eastern mimic, but, so far as we know, never the finished product." These early stages were found in western, the finished product in eastern Uganda,

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* All pages quoted without indication of the original source refer to BEDROCK for October, 1913.

but accompanying the latter is a small percentage of the early stages. A single example (Fig. 13, facing p. 62 of Bedrock for April, 1912) was even captured by Dr. Carpenter on Damba Island in the Victoria Nyanza. It is, therefore, impossible to explain the difference by an appeal to climate; for the abundant finished product and the rare early stages—representing different levels of development—fly together in the same forest patches in eastern Uganda and have often been caught on the same day. The patterns are clearly hereditary and not caused by climate; the differences are small, and together they bridge over the gap between the western female which mimics the males of western *Planemæ* and the eastern female which mimics the male of a Uganda *Planema.*

(3) The theory of mimicry "is driven to argue for an utterly unknown and mysterious process by which these minute variations can be built up into a widely different and fixed form." This objection seems to be in large part a rhetorical re-statement of the first. The "unknown and mysterious process" is Natural Selection, its agents, insect-eating enemies, chiefly and perhaps exclusively birds. That minute variations are, as a matter of fact, "built up into a widely different and fixed form" we can see for ourselves by tracing the females of *Acræa alciope* from the Semliki Valley into Eastern Uganda.

(4) The theory of mimicry "is unable to account for the absence of transitional forms when the germ-plasms of the old form and the new one are mixed." I explain the segregation that occurs by the Mendelian theory, which, I believe, as stated on pp. 309—10, has played an important part in the evolution of mimicry, and especially of those examples in which the females appear in two or more different forms. I find no difficulty in believing that the Mendelian principle operates at many successive stages in the evolution of such resemblances, and I asked Professor Punnett why he preferred to think that it can only act once in the history of a mimetic form, and why he sought to lay this hard burden on the Mendelian principle as a factor in evolution (p. 310). He made no reply.

Within the last few weeks I have received from Mr. W. A. Lamborn a family of *Papilio dardanus* bred from a captured *hippocoon* female. While Mr. Lamborn's six previous families from the same parental form, also from Southern Nigeria, yielded no females except *hippo-*

coon, this last includes six *hippocoon* and eight *dionysus*—a strange ancestral non-mimetic form scattered in relatively small numbers along the tropical west coast. The most probable interpretation of the facts is the assumption that *dionysus* is dominant over *hippocoon* and that the male parent was a heterozygote. Mr. Lamborn exposed some of the pupæ to cold, but this does not explain the fact that all six *hippocoon* are extremely constant, while the eight *dionysus* exhibit the most remarkable variation. *Hippocoon*, on the west coast, in the presence of the predominant model *Amauris niavius*, is abundant, and presents, in spite of minute variations which *are* hereditary, a nearly constant pattern. *Dionysus*, without a model, is rare and excessively variable. The contrast in nature is repeated in the offspring of a single family. It is probable that results of the same kind, but even more striking, will be obtained when *trimeni* is bred on the Kikuyu Escarpment. Professor Punnett implies that, in speaking of this latter form as "specific," he did not claim for it specific rank, but merely meant that it was fixed and definite. I am glad to know his meaning, for the passage misled me as well as other readers. *Trimeni*, however, is remarkable for its want of fixity, and especially for variations which form a transitional series towards the male-like female on the one hand and the *hippocoon* pattern on the other.

(5) The theory of mimicry "has no adequate explanation to offer for the frequent absence of mimicry in the male sex." Wallace originally explained this absence by the probable hypothesis that mimicry is of more value to the female, and therefore more stringently selected in this sex, than in the male. Darwin argued that this hypothesis is by itself insufficient; for why should not the advantage gained by the female be transferred to the male?—"It would be some advantage, certainly no disadvantage, for the unfortunate male to enjoy an equal immunity from danger." Darwin continued: "For my part, I should say that the female alone had happened to vary in the right manner, and that the beneficial variations had been transmitted to the same sex alone." The answer to-day is the same as that given by Darwin and Wallace. Predominant female mimicry is due to the fact that the sex-limited colours and patterns of females are more variable than those of males, and thus more frequently supply the material for selection.

A more stringent selection operates upon more varied material. The variations, being linked with sex, are not transferred to the male.*

(6) The theory of mimicry "leaves without any solution those numbers of cases of polymorphism where there is no question of mimicry." It is unreasonable to suggest that variations which are not mimetic ought to be explained by the theory of mimicry. Neither this theory nor the parent theory of Natural Selection explains variation. It is the other way,—hereditary variation is one chief explanation of Natural Selection and of mimicry. Although we do not know the cause, it is the fact that female butterflies are far more subject to polymorphism in colour and pattern than the males, thus supplying material upon which female mimicry may be built up.

(7) Lastly, the theory of mimicry "endows birds with powers of selective destruction which are certainly not deducible from the available evidence." This objection again is simply the first expressed in different language. I may say, however, that I have never claimed that the direct evidence warranted any such conclusion. It is hardly likely, I think, that such direct evidence will ever be forthcoming, although I hope for the best, and shall not cease to stimulate observation on this special point. We have already a large body of direct evidence that insects with warning colours are distasteful to the majority of insectivorous birds, and that procryptic species are palatable to them. We may reasonably hope for an immense increase in this evidence. There is also some evidence that enemies are misled by mimetic resemblance, and that they remember an unpleasant experience and associate it with the appearance of the object from which it was received. On these lines, too, it is reasonable to expect far more evidence. But I do not think it likely, although of course it is possible, that there will ever be available *direct* evidence of the growth or maintenance of mimetic likeness by means of selective destruction. There is already a great mass of indirect evidence which is increasing at a very rapid rate. I allude to such observations as those of Dr. G. D. H.

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* This question is more fully discussed in *Darwin and the Origin*, 1909, pp. 132—9, where the above quotations from Darwin's letters are given at greater length.

Carpenter, published in the October number of BEDROCK (pp. 359–60)—the fact that the mimetic forms of a polymorphic *Pseudacræa* vary more freely and run into each other more completely on islands in the Victoria Nyanza, where their models are relatively scarce, than they do on the mainland, where their models are abundant. How interesting is the comparison between these observations in Uganda and those referred to on pp. 36, 37, as made by Mr. W. A. Lamborn in Southern Nigeria, where two female forms of *Papilio dardanus* were bred in a single family ; one of them, *hippocoon*, with an abundant model on the west coast—constant ; the other, *dionysus*, an ancestral non-mimetic form—extremely variable. The same difference exists between the wild forms, as may be seen in any good collection from the west coast. No cause, except selection, has been suggested for the relative rarity and variability of the non-mimetic form as compared with the abundance and constancy of the mimetic, and the same comparison holds between *trimeni* and the fully developed mimetic forms of East Africa. Indirect evidence along these and other lines is, as I have said, accumulating steadily and rapidly, and will probably convince the great majority of naturalists.

I now propose to deal with other issues raised by Professor Punnett in his last article.

Of course I agree that " Charles Darwin's work is not beyond fair criticism any more than that of any other man." Weismann's contention that " acquired characters " are not transmitted was a criticism of Charles Darwin's work, and I endeavoured, with others, to introduce it to English zoologists. But this new contention, as it was then, had been investigated with the utmost care and was supported by evidence on the most varied lines. How utterly different is the spirit of Professor Punnett's rash and unsupported assertions. The hereditary transmission of small variations plays an infinitely more important part in the Darwinian theory of evolution than the principle against which Weismann developed his carefully planned and elaborate attack. And Professor Punnett is content to sweep the whole fabric aside without evidence, without critical examination. The dogmatic statement that the inheritance of minute variations is a " sweeping assumption " *does* imply that either Darwin or the speaker is a hasty generaliser ; and it is well to create prejudice against the attempt to settle tremendous issues in this offhand manner.

I pointed out in 1909 that Professor Bateson and Professor Punnett had misinterpreted de Vries to English readers, the former even stating that the Dutch botanist makes a "clear distinction" between "fluctuations" and "mutations"—"clear" forsooth, when the language used was so much the reverse of limpid as utterly to mislead the exponent himself! Until Professor Punnett's last article, in BEDROCK, published in January of the present year, I have seen neither defence nor admission of error on the part of these two exponents of de Vries. Now, however, Professor Punnett does admit that he "may have erred," but maintains that, although de Vries does not make the distinctions he had imputed to him in a popular work intended for general readers—still the distinctions were those which de Vries ought to have made! Indeed, so strongly does Professor Punnett feel this that he tells us he is going to continue to use de Vries' terms, not in the sense in which de Vries uses them, but in that which he wrongly attributed to de Vries. How useful these words will be, and what an aid to clear thinking, in the controversies of the future!

Professor Punnett supposes that I maintain de Vries' "fluctuations" to provide the variational steps by which mimicry was brought about. I stated in the October number (pp. 297, 298) that de Vries' "fluctuation" and "mutation" were the same as Galton's "regressive" and "transilient variation." The "fluctuations" or "regressives," if they exist at all, are clearly not the steps of evolution as they were imagined by Darwin or by the Darwinian to-day. Galton at one time maintained, and de Vries now maintains, that the advance which can be made by these steps soon reaches its limit. The small evolutionary steps on which Darwin relied are the very same variations which some writers would now seek to call "Mutations," as if they were something "new and strange"—variations which Weismann showed to be germinal in origin, and therefore called "blastogenic." These furnish the steps of evolution everywhere, including, of course, the production of a mimetic likeness. When selection ceases, the likeness is soon blurred and, finally, obliterated by the appearance of other germinally caused variations that are no longer eliminated.

I now turn to Professor Punnett's argument that, because the seasonal forms of certain butterflies are capable of being evoked by certain stimuli, the small differences between sub-species or geographical races may be "acquired" by climatic influence. But the former examples were first known to be seasonal because of the times at which they appeared. The latter, too, may differ in their response to seasonal stimuli, but they also differ in other features that appear independently of climate, even when the seasons differ as greatly as in Africa.

Much of the best systematic work of the present day consists in the establishment of these very geographical races, generally distinguished by small differences, but keeping true to their locality. If sub-species are real, then minute variations must be inherited. Professor Punnett suggests that they are unreal. "It seems to me not at all unlikely that the differences are what are often vaguely termed climatic," he says of the local changes in the average size of a spot in *Danaida chrysippus ;* and he must hold the same views for all other small geographical variations if he is to maintain the position that no clear case of such inheritance has been proved to exist. I should have thought that he would have spent many years in breeding experiments before he thus ventured to sweep away the foundations of so much good work. But this is not the method of the present-day writer on evolution. Johannsen weighs beans, de Vries records the variations of Evening Primroses, and instantly, without any further effort, without even troubling to read de Vries himself accurately, the whole foundations of evolutionary thought are assumed to be broken up.

Now that the question has been raised, it will doubtless fall to my friends to make the experiments which will test whether sub-specific characters are real or unreal. Indeed, I have already written to several naturalists on the subject.

In the meantime, there are very strong reasons for rejecting Professor Punnett's suggestions that these local differences are climatic. The fine butterfly *Danaida plexippus* (*archippus*), known in North America as the "Monarch," is a close ally of *D. chrysippus.* It extends through nearly the whole of the American continent, splitting up into at least three geographical races, one in North America, two in the South. There is reason for the belief that it was originally an Old World butterfly, and that it reached America by way of the north. It has at any rate inhabited North America long enough to have produced an exceedingly perfect mimic, while it has wrought no such effect in the South. In spite of its long sojourn in the New World, its pattern still strongly resembles that of its Old World allies. Nevertheless, it has formed geographical races, distinguished from each other by small differences of pattern.

During the past seventy or eighty years this butterfly, probably aided by steam transport, has been spreading to many parts of the Old World, both west and east of America. Commander Walker, who has made a special study of the subject, has kindly furnished me with the dates at which it was first recorded from the following localities :—

First westward : New Zealand, 1840 ; Marquesas Islands, " about 1860 " ; Sandwich Islands, 1845 — 50 ; Caroline Islands, 1857 ; Tonga, 1863 ; Niuafou, 1866 ; Samoa, 1867 ; Tonga Tabu, 1868 ; Rarotonga, 1869 ; Tahiti, 1870 ; Lord Howe Islands, 1870 ; Clarence River, N.S.W., 1871 ; Melbourne, 1872 ; Queensland, 1870 ; Solomon Islands, 1887 ; New Britain, 1895 ; Hong Kong, 1896 ; Straits of Malacca, 1889.

Next eastward : Azores, 1863 ; Canary Islands, 1893 * ; British Isles, 1876 ; France, 1877 ; Atlantic Ocean (200 to 300 miles from the British shore), 1880 ; Atlantic Ocean (sixty miles from Cape St. Vincent), date ? ; Gibraltar, 1886 ; Grecian Archipelago, 1897.

In many of these localities the butterfly has established itself, and is now apparently a permanent resident. In spite of the great climatic differences to which it has been subject in the course of this extensive colonisation, Commander Walker has never seen a record of any except the North American form. The natural inference is that the species is not sensitive to climatic conditions, and that the South American races are not due to this influence.

The eastern and western sub-species of African butterflies nearly always meet and interbreed in eastern Uganda or western British East Africa. How can climate explain the phenomena that are manifest at their overlap—either an abrupt replacement, or, probably

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* The butterfly certainly reached the Canary Islands much earlier than 1893. I saw it myself in Grand Canary in 1888.

more often, a series of transitional variations? Furthermore, in *Danaida chrysippus* itself, although there is a marked geographical difference in the average size of a certain white spot on the forewing, yet in the same locality and at the same time, these spots are seen to vary greatly in size.

Professor Punnett says that he is not prepared to subscribe without reserve to the view that the female of *Elymnias undularis* was originally like the male. He does not discuss, and is probably not aware of, the evidence—very old and well known—which makes this conclusion probable. I remember exhibiting illustrations of the following series in an evening lecture before the British Association in 1890.

A little group of Oriental species and sub-species of *Elymnias*, of which *undularis* is one, presents us with the following sequence: (1) in the Andaman Islands, both sexes alike and resembling all the other non-mimetic males of the group, including *undularis*; (2) in Sikkim and North-East India, also in Ceylon—female mimetic, male non-mimetic; (3) in Burma—female often with white hind wings in mimicry of a Danaine model with white hind wings, male non-mimetic; (4) in South India—female mimetic, male with a pattern intermediate between that of the female and the non-mimetic male of other localities.

Such a sequence will satisfy most naturalists that the hypothesis doubted by Professor Punnett is the only one consistent with the facts. I am very far from denying that in some cases of sexual dimorphism, the male form may be the more recent, but, so far as I am aware, in all examples with mimetic females, the evidence—whenever evidence is available—points in the same direction as that furnished by *Elymnias*. Thus the facts known concerning *Papilio polytes* will be admitted by most naturalists to support the same conclusion. The females are not, as Professor Punnett implies, constant and invariable. They vary greatly in the same locality, and still more in the different parts of their geographical range. The male pattern is far more constant, although it too undergoes recognisable geographical changes. Furthermore, it is not only more constant than the female, but it resembles the pattern of other allied species. Such resemblances between species have hitherto been accepted as evidence of descent from a common ancestor. In other words, patterns like those of the male *polytes* have been regarded as ancestral, as compared with their females, which, diverging in various directions, resemble the patterns of remote species. In the most eastern part of the range on the Asiatic mainland, the *aristolochiæ* models are distinguished by the small size of the white patch on the hind wing. The mimetic females follow them. In Borneo and Sumatra *aristolochiæ* is represented by *antiphus*, without any white spot. The mimetic females follow them, although a small trace of the spot is present in some individuals.

In BEDROCK for last October it was argued (p. 309) that the red submarginal spots of the mimetic females were derived from those already present on the under, and occasionally on the upper, surface of the non-mimetic male. I have lately re-studied this question with a much larger series of individuals and have found additional evidence pointing to the same conclusion. One spot in the series—that below vein 4—is nearly always much smaller than those on either side of it and sometimes it is altogether wanting when they are present. This relationship is commonly found on the under surface of the males and male-like females, and on the upper surface also, when these spots are present,—as they are far more commonly in the male-like females than in the males. The same relationship is also common on both surfaces of the *polytes* females as well as of other mimetic female forms. It is less often seen and less striking in the *hector* form (*romulus*) than in the *polytes* form from the same locality, corresponding with other evidence, based on the evolution of the pattern, which indicates that the former is further removed from the ancestral appearance of the male than is the latter.

I have never contended, as Professor Punnett asserts (p. 571), that because the difference between the patterns of the mimetic and non-mimetic females of *polytes* is "somewhat complex," it cannot have arisen as a single mutation. I grant that a large and complex variation may arise. Professor Punnett passes over the real improbability—the sudden origin of a complex pattern which matches that of another and remote species. The same difficulty is encountered by the hypothesis that the mimetic females of *Elymnias* arose suddenly.

We know that the mimetic and non-mimetic females of *polytes* are produced without intermediates, and the question is whether they developed by a series of stages or suddenly arose in their present form. In the course of this discussion, Professor Punnett triumphantly pointed to the admitted fact that they do so arise! It was this mode of argument that I ventured to parody in a travesty taken too seriously by Professor Punnett.

I stated in October, 1913, that I had always recognised that the first variation which initiates mimicry must be something appreciable, and proceeded to prove it by quoting a striking example from my article in BEDROCK for April, 1912. I even complained, and justly, that Professor Punnett had altogether misrepresented me. The only reply that he now makes is triumphantly to assert that the views expressed and illustrated in April, 1912, were "elicited" by his article in July of the following year. I suppose he will now claim that the earliest statement of the kind I remember to have made* —in 1890—was elicited by him!

There is nothing inconsistent between these views upon the origin of mimicry and the passage quoted from *Darwin and the Origin*, by Professor Punnett. I do not regard the "first colour change" which started mimicry as a large variation, or one that differs from the steps of evolution as Darwin postulated them.

I am reminded, by Professor Punnett's particoloured rabbits, of the hooded rats figured by Professor W. E. Castle (*Heredity and Eugenics*, Chicago, 1912, p. 58). Here is a Mendelian investigator who has been led by his experiments to believe that "Mendelizing characters can be modified by selection," and I bring this article to a close by quoting part of the concluding paragraph of his lecture:—

> "Accordingly we conclude that unit-characters are not unchangeable. They can be modified, and these modifications come about in more than a single way. Occasionally a unit-character is lost altogether or profoundly modified at a single step. This is mutation. But more frequent and more important, probably, are slight, scarcely noticeable modifications of unit-characters that afford a basis for a slow alteration of the race by selection. . . ."

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* *Nature*, October 2nd, 1890. Reprinted in *Essays on Evolution*, 1908, p. 376.

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Report, p. 519.

[Uncorrected Proof.]

The term 'Mutation.' *By* Professor E. B. Poulton, *F.R.S.*

1. The word 'Mutation' was originally introduced by Waagen[1] to express a simultaneous and probably gradual change in a relatively large proportion of the individuals of the species, if not the whole species. 'Mutation' expresses the change itself, not the process by which it has been produced. Waagen nowhere states that his 'Mutations' are discontinuous variations or 'Saltations.' Waagen's material was exclusively palæontological, and his 'Mutations' are variations in time. He was inclined to believe that they were produced by a developmental force resident in the organism.

2. 'Mutation' was re-introduced by de Vries as equivalent to 'Saltation,'[2] and applied to Darwin's 'large' or 'single' variations as opposed to his 'individual differences.' The latter de Vries called 'Fluctuations.' According to de Vries as well as Darwin *both forms of variation are hereditary.* De Vries distinguished between them by supposing that a 'Mutation' leaps at once to a new position of genetic stability—it is what Galton previously called 'transilient.' De Vries' 'Fluctuations,' on the other hand, are subject to Galton's 'regression to mediocrity,' and there is a limit to the advance which can be achieved by selection.[3] It must be added that de Vries is disposed to explain 'Fluctuations' as due to the action of the environment, and, so far as they are concerned, to accept the 'hereditary transmission of acquired characters.' The majority of biologists will prefer to conclude that de Vries' 'Fluctuations' are of two very different kinds, some of them being (*a*) Germinal characters that are hereditary, and subject to Galton's 'Regression'; and others (*b*) Somatic characters that are not hereditary. De Vries uses the term 'Mutation' to express (1) a single 'Saltation' and (2) the theory that evolution progresses discontinuously by means of 'Saltations.' He states, however, that his 'Mutations' may be small.[4]

3. Bateson, Punnett, Shipley and others have erroneously stated in recent years that de Vries 'pointed out the clear distinction between the impermanent and non-transmissible variations which he speaks of as *fluctuations,* and the permanent and transmissible variations which he calls *mutations.*'[5]

In this third use of 'Mutation'—Batesonian, not de Vriesian—the word is applied to any and every hereditary character and becomes the same as Weismann's 'Blastogenic Variation.' 'Fluctuation' similarly in this second use, restricted to (*b*) as explained above, becomes the same as Weismann's 'Somatogenic Variation.'

This mistaken reading of de Vries has unfortunately been widely followed, so that the Dutch botanist is now generally credited in this country with the bestowal of Waagen's term 'Mutation' upon a form of variation previously announced by Weismann, instead of upon one ('Transilient') previously announced by Galton.

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[1] 'Die Formenreihe des *Ammonites subradiatus,* &c.' *Geogn.-palaeont. Beiträge* ii, Heft 2, b (1869), p. 186.

[2] *The Mutation Theory,* Engl. Transl., Vol. i, London (1910), p. viii. 'These saltations, or mutations. . . .'

[3] *Ibid.* p. 123:—'Continued selection [of fluctuations] by no means fixes the character chosen, but, by separating the race further from the type from which it sprang, continually adds to the risk of regression.' This is precisely Galton's conclusion, just as 'Regression' in this sense is Galton's term. Darwin also 'fully recognised the limits which may be set to the results achieved by the artificial selection in one direction of individual variations,' and 'he admitted the necessity of waiting for a fresh "start in the same line."' (*Darwin and the Origin,* Poulton, London (1909), pp. 48, 49).

[4] *Ibid.*, p. 4.—'Of course every peculiarity of an organism arises from a previously existing one; not however by ordinary variation, but by a sudden though minute change, ... The name I propose to give to this "species-forming" variability is Mutability. . . . The changes brought about by it, the Mutations, ...'

So also on p. 55:—'. . . many mutations are smaller than the differences between extreme variants' [here used as equivalent to 'Fluctuations.']

[5] *Mendel's Principles of Heredity,* Bateson, Cambridge (1909), p. 287.

The existing hopeless confusion can only be set right by restoring the term 'Mutation' to its rightful owner Waagen—a measure of justice for which geologists have been contending for several years.[6]

For the two other uses of 'Mutation' and for the two kinds of 'Fluctuation' the following changes are suggested :—

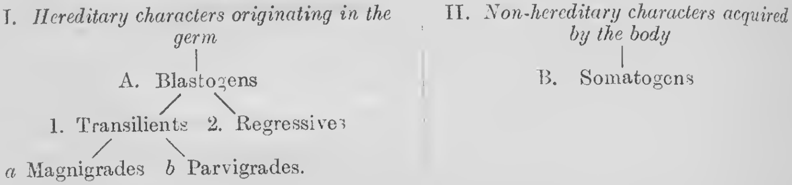
For 'Mutation' II. (de Vries), both large and small, substitute Galton's 'Transilient,' used as a substantive. The old associations of 'Saltation' are always with large variations, and the term should never be applied to small 'Transilients.' The term 'Magnigrade' to be used as substantive or adjective, may be conveniently applied to a 'Saltation' or 'Large Transilient,' 'Parvigrade,' similarly to a 'Small Transilient.' 'Magnigrade Evolution' is 'Discontinuous,' 'Parvigrade Evolution' 'Continuous.'

For 'Mutation' III. (Bateson *nec* de Vries) substitute 'Blastogen,' the substantive form of Weismann's 'Blastogenic.' Other synonyms are 'Constitutional,' 'Congenital,' 'Genetic,' 'Inborn,' 'Innate,' 'Inherent' and 'Centrifugal.' The term 'Variation' has also been used in this restricted sense.

For 'Fluctuation' I(*a*) (de Vries) substitute Galton's 'Regressive,' used as a substantive.

For 'Fluctuation' II. (Bateson) = I(*b*) (de Vries) substitute 'Somatogen,' the substantive form of Weismann's 'Somatogenic.' Other terms are 'Acquired' (going back to Erasmus Darwin, 1794, and Lamarck, 1809) antithetical to 'Inherent,' 'Centripetal' to 'Centrifugal,' and 'Modification' to 'Variation.'

The relationships are shown below :—


I. *Hereditary characters originating in the germ*
A. Blastogens
1. Transilients
2. Regressives
a Magnigrades
b Parvigrades.
II. *Non-hereditary characters acquired by the body*
B. Somatogens

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[6] F. A. Bather in J. E. Marr's Presidential Address to the Geological Society of London, 1905, *Proceedings*, pp. lxxii, lxxiii. In drawing up the present abstract I have received much kind help from my friend, Dr. Bather.

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60.—THE PROPORTIONS OF THE FEMALE FORMS OF *PAPILIO POLYTES*, L., IN THE DIFFERENT PARTS OF ITS GEOGRAPHICAL RANGE.

By EDWARD B. POULTON, D.Sc., F.R.S., *Fellow of Jesus College, Oxford, and Hope Professor of Zoology in the University.*

The investigation here suggested is of great interest and importance and at the same time very easy to carry out. All that is required is to breed the butterflies from indiscriminately collected larvæ in each locality and send the specimens to me at the University Museum, Oxford, so that they may be sexed and recorded. Additional value will be given to the investigation by obtaining as full and accurate a record as possible of the relative proportions to each other and to their mimics in the same locality of the two models, *Papilio hector*, L., and *P. aristolochiæ*, F. If it be found impossible to breed the forms of *polytes*, interesting results may be gained, although of much less value, by the indiscriminate collection of the butterflies, particularly if all or as nearly as possible all the specimens seen on any given occasion are taken.

A short abstract of the results already obtained will show the great need for further investigations.

Ceylon. Mr. J. C. F. Fryer has recorded in *Phil. Trans. Roy.Soc., Lond.*, Series B, Vol. 204 (14th November 1913), p. 249, the results of breeding from 155 indiscriminately collected wild larvæ, *viz.*, 66 males, 40 male-like females (*cyrus*, Hubn.), 24 *romulus*, F., females mimicking *P. hector*, and 25 *polytes*, L., females mimicking *P. aristolochiæ*. It is suggested that these results may be significant.

"In Ceylon, therefore, if the above statistics are reliable, the ratio between the mimetic and non-mimetic females is one which might be expected if it be assumed that there is no selection in favour of either of these forms of female; under these conditions the population is stable in composition and may remain so indefinitely.

"On the whole question, however, no final conclusions can yet be drawn, for, in the first place, the numbers obtained from the statistics may quite possibly be a coincidence, while in the second the effects of the phenomena discovered in connection with the fertility and mating of the species are quite unknown. Possibly the conclusion which can be drawn with the greatest confidence is that the extraordinary mimicry in the female sex is at present of little importance to the population of the butterfly in Ceylon. (*Ibid*, p. 250)."

I have not at present been able to set beside Mr. Fryer's ratios those derived from breeding in other areas but the following evidence, quoted in all cases from the *Proc. Ent. Soc. Lond.*, goes far to disprove the general application of the conclusions set forth in the above-quoted paragraphs.

West slopes of Ashamboo Hills, North-West of Cape Comorin. In this locality in the extreme south of India, J. Williams Hockin collected (1905-16) 30 males, 1 *cyrus* female, 12 *polytes* females, 21 *romulus* female, 1 female intermediate between the last two. Of the 12 *polytes*, 4 were *stichius* with no white in the hindwing cell, 4 *polytes* with conspicuous white, and 4 intermediate. The female intermediate between *polytes* and *romulus* was an interesting form, indistinguishable from some of the forms of *theseus*, Cramer, from Borneo. As regards the models Mr. Hockin considered *hector* decidedly commoner than *aristolochiæ* and indeed the commonest *Papilio* in the district, *aristolochiæ* being second, and *polytes* third "but several lengths behind." (1917, lxxx-lxxxiii.)

The Ceylonese *polytes* females, although in a closely adjacent area, are very different in that the *stichius* form is almost unknown while the hind-wing cell of the great majority is conspicuously white-marked, a fact which, it can hardly be doubted, is related to the abundance in Ceylon as compared with India of forms of *aristolochiæ* with a white cellular spot in the hind wings (Rothsd. and Jord., *Nov. Zool.*, II, 1895, p. 248).

North Kanara. According to the extensive experience of T. R. Bell, largely derived from breeding, the *cyrus* form is excessively rare; it was in fact only once obtained and then by capture. Of the two mimetic forms, both abundant, *romulus* was perhaps the commoner. (1914, xcix-c.)

Neighbourhood of Madras City. Out of 45 females taken on two days in 1915 by Prof. and Mrs. Fyson, 23 were *polytes* and 22 *romulus*;

34 males were also captured. Twelve *hector* were taken and, on another day, one *aristolochiæ*. (1915, xcii-xciv.)

Singapore Island. In 1916 Dr. R. Hanitsch collected 27 males, 8 of the *cyrus* female and 9 of the *polytes* female together with 5 of the models of the latter. (1916, lxxvi-lxxviii.) Later in the same year he collected 34 males, 5 *cyrus* and 9 *polytes* (1917, xxx-xxxiv.)

The mainland (Johore) opposite Singapore Island. Dr. R. Hanitsch received from his collector 12 males, 3 *polytes* female and 1 *cyrus* female (March 1917), and a second example of the *cyrus* female (July 1917) together with 3 males taken on the same day and 8 males somewhat earlier. (1917, xxx-xxxi, lxxxiii-lxxxiv.)

These results from Singapore and mainland are very different from those recorded by Dr. Seitz who only remembers the *polytes* female in this locality. (1913, p. xxxii.)

The Hongkong and Macao Districts. The male-like female *cyrus* is, on the evidence of most naturalists, much the commonest form of the mimetic forms; *romulus* is unknown and the *polytes* female rare, as is its model, *aristolochiæ*. Of 10 examples from Stonecutter's Island in Hongkong Harbour 4 were males and 6 *cyrus* females. (1913, xxxi-xxxiii.)

I think it will be agreed that the results summarized above are sufficient to show how important it is to obtain evidence on a more extensive scale, and especially to carry out, in as many localities as possible, Mr. Fryer's method of breeding from indiscriminately collected larvæ.

Mr. Fletche

I suppose that you all know that *Papilio polytes* is remarkable in having three forms of female, all different from one another. There is firstly the form *cyrus*, which is like the male, secondly the form *polytes* which resembles *Papilio aristolochiæ*, and thirdly the form *romulus*, which mimicks the female of *Papilio hector*. I have here specimens [*exhibited*] of these forms of females and of the two other *Papilios, P. aristolochiæ* and *P. hector*, which they mimick.

We at Pusa have tried some breeding experiments with *Papilio polytes* and I have here [*exhibited*] specimens of two generations reared from a captured female. As you will see, the females reared in this lot belong to the forms *cyrus* and *polytes*. We have not bred any *romulus* here as yet, although *romulus* does occur rarely at Pusa. In this connection I may note that *Papilio hector*, the model for the *romulus* form, does not occur at Pusa; I have seen it from Nagpur, where it is rare, but from nowhere north of that.

It will be of considerable scientific interest if any of you can assist by rearing *Papilio polytes* in numbers from known parents and sending the resulting specimens either to Pusa or direct to Professor Poulton. It is not easy to rear them in numbers; at least, we have not found it possible at Pusa to rear more than two generations, so far.

If you will collect specimens of *P. polytes*, taking indiscriminately *all* the examples seen at one time in any one place of *P. polytes*, *P. hector* and *P. aristolochiæ*, that will also be useful, as giving us an idea of the relative proportions of occurrence of the different female forms and of the species which they resemble.

Another *Papilio* which would well repay breeding in numbers is *Papilio memnon* which has numerous distinct forms of females, some tailed and some tail-less. In Java both tailed and tail-less forms have been bred from one batch of eggs, but I do not think that *P. memnon* has ever been reared on any scale in India.

I am sure that I am endorsing the feelings of this Meeting in saying how grateful we are to Professor Poulton for sending us this paper.

SGPI—M—98 AA to G. of I—24-12-20—50.

Reprinted from the Report of the Proceedings of the Fourth Entomological Meeting held at Pusa, 1921.

34.—THE PROPORTION OF THE FEMALE FORMS OF *PAPILIO POLYTES*, L., IN DEHRA DUN, UNITED PROVINCES, AND BIHAR.

By Edward B. Poulton, D.Sc., F.R.S., *Fellow of Jesus College, Oxford, and Hope Professor of Zoology in the University.*

The little paper on the proportion of the female forms of *Papilio polytes*, L., read and kindly emphasized by Mr. T. Bainbrigge Fletcher at the Third Entomological Meeting at Pusa, in February 1919 (Report, Vol. III, pp. 903-906) has produced a most interesting series of *polytes* captured in 1919 and 1920 by Mr. C. M. Inglis at Baghownie, Laheria Sarai P. O., B. & N.-W. Ry., towards the south of the Darbhanga District of Bihar. I therefore take the opportunity of contributing a preliminary study of this material to the Fourth Entomological Meeting at Pusa. Furthermore, a fine series captured by Mr. O. C. Ollenbach at Dehra Dun, United Provinces, in March 1917, only reached me after the Third Entomological Meeting had taken place, the captor wisely deciding to avoid any unnecessary risks in transport. This series also has been studied and the results are submitted together with those from Baghownie.

Mr. Inglis' captures were all made within two miles of Baghownie and all were taken and sent, whether damaged or not. The injured specimens are of great interest being in nearly all cases symmetrically shorn, or torn at the anal angle of the hind wing, injuries evidently the work of birds or lizards. In a few cases as much as half one or both hind wings has been shorn away. In addition to the *romulus* forms recorded in the table on page 261, Mr. Inglis captured it on July 31, 1917, and September 2nd and 9th, 1918. Concerning the models he wrote on February 9th, 1920 :—

"*hector* itself is never caught. *P. aristolochiæ* is of course, a common species here. The earliest I have noticed appears to be May 29th, but it is not till the middle of July that they can be said to be common. August also seems to be the month during which most are got, the same as *polytes*."

Also on July 10, 1920:—

'Mr. Bainbrigge Fletcher writes. 'I should think we are roughly 400-500 miles beyond the range of *Papilio hector*. The elevation at Pusa is about 150 feet above sea-level.' These words would also apply to this place which is not very far from Pusa. We are evidently a little closer to the *hector* range than Dehra Dun and the *romulus* form is slightly stronger here" (see the table on page 261).

Concerning the Dehra Dun series Mr. Ollenbach wrote in September 17th, 1919:—

"I made no choice but took all that came, so far as I was able to. The *romulus* form is certainly very uncommon here and *P. hector* does not occur. The nearest parts of its range are about 800 miles to the East and the same distance to the South. *P. aristolochiæ* is plentiful here now, though some twenty years ago it was not to be seen."

On this last interesting point he wrote again on March 10th, 1920:—

"I cannot quite remember when *P. aristolochiæ* first appeared in Dehra Dun, but probably about twenty-five years ago. I have a specimen in my collection taken in the year 1895. They had probably only just appeared at that time and were very scarce, although now they are just the reverse; *aristolochiæ* is however by no means so numerous as *polytes*, which is a very common species."

In 1920 Mr. Ollenbach, was unable to continue to collect *polytes* in Dehra Dun because "for some unknown reason this butterfly and *P. aristolochiæ* were very scarce although in ordinary seasons they were very common."

In the following tabular statement I have classified the *polytes* females in four groups according to the absence or presence, and degree of development, of the white spot in the hind wing cell. The transition between *stichius*, with no white in the cell, and *polytes*, possessing it, is complete—so much so that all those specimens in the fourth column of the table and some of those in the fifth would, unless carefully examined, be placed in the third as typical examples of *stichius*. The white mark in the cell of such individuals is only represented by scattered scales often less than a dozen in number. The comparisons which formed the basis of the table were made upon the under-surface of the wings only but it is not anticipated that an examination of the upper-surface would lead to any change.

Dates in 1919, 1920 at Baghownie, Bihar.	Males.	Male-like *cyrus.*	FEMALE FORM POLYTES (INCLUDING STICHIUS) MIMICKING PAPILIO ARISTOLOCHIÆ.				Female form *romulus* mimicking *Papilio hector.*
			No white in H. W. cell *stichius.*	Minute trace of white in H. W. cell.	Small white spot in H. W. cell.	White spot in H. W. cell large to moderate.	
1919, July . .	7	1	2	0	2	3	2
„ August . .	23	5	6	3	3	3	0
„ September .	7	3	6	0	1	3	1
„ October. .	9	2	6	1	2	0	0
1920, March . .	5	0	1	0	0	0	0
„ April . .	4	1	0	0	4	1	0
„ June . .	4	0	1	0	1	0	0
„ July . .	11	7	8	1	4	12	0
„ August . .	4	0	6	2	7	4	1
„ October. .	31	10	8	2	11	6	1 (seen)
TOTAL .	105	29	44	9	3~~4~~5	32	5
	Total 124, including 4 additional females.						
In 1917 at Dehra Dun, United Provinces.	The above total from Baghownie, S. Darbhanga District, Bihar, to be compared with those below, from Dehra Dun, United Provinces.						
1917, September .	149	38	15	0	10	10	1
	Total 35 females of form *polytes.*						

In addition to the specimens tabulated above, three females of the *polytes* form were taken at Baghownie in August and October 1919 and October 1920, respectively but all so much injured in both hind wings that they could not be assigned to their proper columns. A fourth female of the same form would have appeared in the fifth column but for the accidental omission of data. It arrived in a consignment containing specimens taken from March to July 1920. The following additional males were also taken :—4-12 November 1919, 4 ; 10th May 1919, 1 ; 1 November 1920, 2.

A few additional specimens were taken at Dehra Dun in the years 1917 to 1919, the most interesting being a *romulus* female on 11 September 1919.

Comparing the two localities by the aid of the figures in the table the chief difference is to be found in the proportions of the male-like female form *cyrus*, outnumbering the *polytes* form at Dehra Dun, but less than a quarter of the same form at Baghownie. This difference would be somewhat diminished but would remain great if we allow for the fact that more males were taken at Dehra Dun and make the reasonable assumption that more *cyrus* would have been taken with an increased number of males at Baghownie. The true proportions can only be ascertained, as Mr. Fryer has rightly maintained, by breeding from indiscriminately collected larvæ and it would be deeply interesting to check the results shown in the above table in the manner. I sincerely hope that this may be possible in both localities.

The great difference between the proportions of the *cyrus* and *polytes* female forms in the two localities may probably be explained by the absence, until recent years, of the *aristolochiæ* models at Dehra Dun and by similar reasoning we may expect a gradual increase in the proportions of the *polytes* f., now that the model has become common there.

The other exceedingly interesting difference, already referred to by Mr. C. M. Inglis (p. 260), is in the proportions of the *romulus* f., to be doubtless explained, on the lines suggested by him, as the result of the much greater distance of Dehra Dun from the range of the model *P. hector*.

I trust that an attempt will be made to breed from one of those rare female forms at both localities. The following considerations make it almost certain that the great majority of them are heterozygotes (hybrids) bearing the pattern of the dominant, and the most probable mating will have been with a male bearing the *polytes* or *cyrus* tendencies (both recessive to *romulus*). The commonest result to be expected would therefore be approximately half *romulus* females (heterozygotes) and half *polytes* females (recessives), or half *romulus* and half *cyrus*.

The reason why the rare *romulus* forms are likely to be heterozygotes is as follows: The handing on of the mimetic pattern from a region where it and its model are common, is probably brought about by wandering males, although sometimes by regular seasonal or exceptional migrations. When a male bearing the tendency of *romulus* thus reaches a population in which the *romulus* female is rare or absent it will rarely or never pair with such a female but with *polytes* or *cyrus*, or the *polytes*-like heterozygotes combining the two. In each case the offspring will be heterozygotes, the females bearing the appearance of *romulus*, the survivors of these again will generally pair with males bearing the common recessive female patterns, yielding again half heterozygotes and half recessives. And even when the rare heterozygotes *romulus* female meets and mates with the equally rare male and produces offspring of which a quarter are pure dominant *romulus*, the survivors of this will at once tend to mate with the common male, yielding again heterzygotes bearing the *romulus* pattern. Therefore, in areas far removed from the range of *hector* where *romulus* is abundant such rare *romulus* forms as are found will be nearly always heterozygotes and only very rarely pure dominants.

The above reasoning was applied to the more complex case of *Papilio dardanus*, in Africa and was subsequently confirmed by breeding experiments in many parts of the range where rare female forms were found to behave as heterozygotes (*Proc. Ent. Soc. London*, 1914, pp. LXVIII—LXX).

The proportion of the *stichius* form to the true *polytes* females does not differ greatly in the two localities ; for the 9 Baghownie examples on the 4th column are *very nearly stichius* and, unless carefully examined, would be assigned to this form. It will be interesting to study in a similar manner the development of the chief hind-wing markings of *aristolochiæ* in various localities and determine whether there is any correspondence in this respect between it and mimetic *polytes*. That this is not unlikely is shewn by the strong development of this marking of both model and mimic in Ceylon, where the *stichius* form is excessively rare (*Rep. Proc. 3rd Ent. Meeting, Pusa*, 1919, p. 904).

Another point of great interest brought out by a careful comparison of the *polytes* females from both localities is the existence of a small proportion of individuals with the hind-wing pattern intermediate between that of *polytes* and *romulus*. The proportion of these in localities where *romulus* is commoner would be well worth studying. It is probable that such individuals are heterozygotes exhibiting imperfect dominance, but this suggestion can only be tested by breeding.

The further investigation of this interesting example of female mimicry will, I think, be assisted by bringing together all the significant references to *polytes* and its models in the publications of the Bombay Natural History Society. I owe these to the kind help of Mr. C. M. Inglis and Dr. R. Hanitsch. In the critical remarks on some of the references I have been kindly helped by Dr. Karl Jordan. A few observations from other publications or hitherto unrecorded have been added.

The references are arranged according to the localities starting from the South of India, proceeding northward and then eastward into Burma and China. References which mention only volume and date are all from the *Journal of the Bombay Natural History Society*.

The following early reference to this example of mimicry occurs in a paper by Colonel Charles Swinhoe (Vol. II, 1887, p. 173) :—" *P. pammon* (*polytes*) the female of which mimics two species, *P. diphilus* and *P. hector*, and in the Nicobars the female of the variety *nicobarus* mimics the Nicobar variety of *P. diphilus*, called *P.* (*aristolochiæ*) *camorta*." *P. diphilus*, Gray is a synonym of *aristolochiæ*, F. Rothschild considers that *nikobarus*, Feld., cannot be separated from the Indian *polytes*. (*Nov. Zool.*, Vol. II, 1895, p. 347). It is however retained as a sub-species by Jordan (Seitz, *Oriental Papilionidæ*, p. 61), who states that "the female form similar to the male appears to be commoner than in other districts."

The range of *Papilio hector*, L., is given by Rothschild (*ibid*, p. 234) as "Ceylon, S. India, Madras, Central Provinces, Calcutta." In Ceylon and Southern India it "is very common at low elevations; farther north it becomes rarer, and does not seem to go beyond the 25th degree of N. Lat." Jordan also states that it is "recorded from Chittagong on the north-east side of the Bay of Bengal" (Seitz, *ibid*, p. 34).

The range of the *romulus* female of *polytes*, mimicking *hector*, is thus defined by Rothschild (p. 347) "Ceylon, South India, Bengal, and occasionally in Sikkim." Jordan gives it as "Ceylon to North India; in Sikkim, where *hector* does not occur, *romulus* is scarce and further east it has not yet been observed at all...." (Seitz, *ibid*, p. 61). The facts recorded in the earlier pages of this memoir prove that *romulus* occurs in small numbers very far east of Sikkim.

The localities now start from the South of India, as already explained. The records published in *Proc. 3rd. Ent. Meeting, Pusa*, 1919, (pp. 904, 905) should be taken into account together with those in the earlier part of the present paper.

Palni Hills. Captain W. H. Evans, (Vol. XX, 1910, p. 384—

"74. *Papilio polytes*. Common at low and often seen at high elevations probably all the year."

"70. *Papilio hector*.
"71. *Papilio aristolochiæ*. } Common at low elevations; May, June, August to October; *hector* is often seen at the highest elevations."

Bangalore. K. Kunhi Kannan. (Vol. XXI, 1911, p. 699) says that the species is trimorphic in Bangalore.

Bangalore District. T. H. L. Grosvenor. (*Ent. Record*, 1920, p. 201.).

P. hector is "abundant everywhere,...... apparently continuously brooded, as from March to December they were always to be found in every possible condition. This was the only *Papilio* I found of which both sexes were commonly taken......at the approach of dusk they settle for the night usually in small colonies of 5 or 6, and apparently return to the same tree each evening. I watched one for over a fortnight, having selected it for observation on account of a crippled hindwing so that there was no chance of mistaking it. One afternoon I saw this insect at the farther side of the plantation at least a mile away but it came back to its usual tree for the night ...." *P. aristolochiæ*, Mr. Grosvenor noted, was "not nearly so abundant in the Bangalore district as *P. hector*, but in the Central Provinces it is in great numbers, and there replaces *P. hector*." *P. polytes*: "Perhaps the most general and abundant species of the Indian *Papilios*. The male is to be seen everywhere, but the interesting polymorphic female is very difficult to find, as it seldom if ever flies in the open, and has to be searched for in dense bushes, and when found is generally torn to rags." All three forms of female were taken, and......"The prevailing form is that resembling *aristolochiae*." Concerning the likeness to the models the author remarks. "It is difficult to see what advantage is gained by mimicry, as the habits of *polytes*, *hector* and *aristolochiæ* are entirely different, and one never has the slightest doubt as to which species one sees, although so closely resembling one another in colour and markings. It certainly does not protect *polytes*, as I have on several occasions seen the King Crow (*Dicrurus ater*) not only attack, but eat it."

The author in writing his last quoted sentence seems to have forgotten the fact that *all* species, protected or unprotected, have their enemies, and that *complete immunity* only existed in the mind of Erich Haase and never in nature. Nevertheless I agree with the author in believing that the ordinarily accepted interpretation of mimicry in *P. polytes* is erroneous, and it seems worth while to reprint here a Statement I wrote several years ago for a journal now out of print ("*Bedrock*," Vol. II, No. 3, Oct., 1913, pp. 310-312) :—

"How can we account for the evolution of two mimetic forms in a butterfly which remains dominant when its models are absent or excessively rare ? It is worth while to consider this question in some little detail, for I believe that the true explanation is different from that usually given.

"*Papilio polytes* is an unusually dominant and successful swallow tail. Its rate of reproduction, combined with a probable measure of distastefulness advertised by a conspicuous pattern, its powers of flight, alertness, and other adaptations of many kinds, keep up the large average numbers in spite of the attacks of enemies of all sorts in all the stages of its life-history. The large numbers that survive in every generation will of course, include the fittest, and so the high level of protection efficiency is maintained. This is the condition of *polytes* in the Hong Kong and Macao districts where the single model (*aristolochiæ*) is so rare that it is unreasonable to suppose that it exerts any effect, and this was doubtless its condition before the evolution of the mimetic forms. There is no reason to suppose that the surviving percentage of *polytes* was increased by the presence of the *aristolochiæ* model or during the growth of the mimetic likeness. All that happened was this :—Certain variations formerly unselected, now tend to fall into the surviving percentage, and, once started, the further stages of transformation were effected in the same way. Each change that suggested still more strongly an advertisement common to a far more distasteful form would tend to be selected. So too, when *polytes* spreads beyond the range of *aristolochiæ,* or when the model for some reason disappears from an area in which *polytes* is abundant, the constitution, not the amount, of the surviving percentage is changed. The mimetic pattern soon disappears, although the species that bore it remains as abundant as before. The survival or extinction of the species is not affected: all that has happened is the survival or extinction of a pattern borne by a certain proportion of the individuals of the species. When these disappear other individuals with another pattern take their place. It is, furthermore, extremely probable that selection is reversed when the models are absent, for a female that resembles the male is better advertised than one which resembles a non-existent model. Although I believe that many mimicking species bear the above-described relationship to their models, I do not mean to imply that this is always so. No doubt there are plenty of mimicking species which depend upon the presence of the model for their existence and could not live in areas from which the model disappeared."

I should perhaps, add that we can well understand the advantage of a mimetic pattern, even when accompanied by great differences in flight and behaviour, if we look upon it as an aid to memory of enemies, helping them to recall an unpleasant experience, rather than as the deceptive resemblance of a palatable eagerly sought-for species to one unpalatable and avoided. Furthermore the difference in flight means for *polytes* powers of escape from those enemies which would devour it but not its model.

North Kanara District. J. Davidson, T. R. Bell and E. H. Aitken. (Vol. X, 1895-97, p. 580). "*P. polytes* : This is very common and very destructive to orange and lime trees in gardens......"

The Konkan. E. H. Aitken and E. Comber. (Vol. XV, 1903-04, p. 52) "*Papilio pammon,* L. Quite common all over the district. Of the several forms of females the *polytes* type, which resembles *P. aristolochiæ,* is the commonest and the *romulus* type is not rare, but we have no record of the form that is similar to the male."

The Konkan. G. W. V. de Rhe-Philippe. (Vol. XVIII, 1907-08, p. 884) " *Papilio polytes* L. I have to record a fourth type of female intermediate between the " *romulus* " and " *polytes* " types. It has the discal markings on the hind wing *white* as in the ' polytes ' form, but at the same time approaching the ' *romulus* ' type in having the broad white band on the forewing. The specimen, which was taken at Khandala in October 1905, is the only one of the kind I have seen."

Bombay Presidency. E. H. Aitken. (Vol. II, 1887, p. 36). " *P. pammon.* This is nearly as abundant as the last (viz., *P. erithonius*), the *polyctor* form of the female being decidedly the most common." Dr. Jordan agrees with me in concluding that " *polyctor* " was inadvertently written instead of " *polytes*."

Nimar District, Central Provinces. D. O. Witt. (Vol. XIX, 1909-10, p. 569).

Papilio polytes, L. " More common in forest areas than in gardens and cultivated land. Of a skulking habit, keeping usually to forest with bushy undergrowth in it. Rains and cold weather."

Central Provinces. J. A. B. (*i.e.*, Betham). Vol. VI, 1891, p. 329.) " 113. *Papilio polytes*, L. This and *P. pammon* are one and the same species. It is the common black and white " swallow-tail " to be found almost everywhere.........It has 3 forms of female, the first almost exactly resembles the male ; the second is a mimic of *P. aristolochiæ*, and the third imitates *P. hector*————."

Plains of India. T. R. Bell. (Vol. XIX, 1909-10, p. 33).

Refers to *P. polytes* imitating *P. hector* and *P. aristolochiæ*.

Plains of India. T. R. Bell. (Vol. XXI, 1911, pp. 527 and 531).

(p. 527). " 83. *Papilio polytes.* A polymorphic form. The male varies slightly but is fairly constant throughout its range ; the female generally with two forms, in Southern India with three, strikingly different in appearance " (with detailed description and plates).

(p. 531). " Another extraordinary thing is that where local forms of *P. aristolochiæ* occur, there the *polytes* form is also modified in a more or less similar way. Things go even further than that in Celebes where typical *polytes* males do not exist, being replaced by a constant similar but aberrant race called *P. polytes alcindor*, Oberth., ; the female is only of one type and that imitates a butterfly of the *P. hector* group called *P. polyphontes*, Boisd, which is only found in Celebes and some few neighbouring islands of the Gilolo group ; and this although *P. aristolochiæ* exists there. Why ? It is difficult to even guess at an answer."

Dr. Jordan kindly informs me that, although *aristolochiæ* was recorded from Celebes by the Hon'ble W. Rothschild (*Iris*, 1892), the single male on which the conclusion was based came in reality from Bali, Doherty having erroneously included some specimens from this island in his Celebes collection. No *aristolochiæ* is known from Celebes. *P. polyphontes* is very common there.

Lucknow District. Geo. W. V. de Rhe-Philippe. (Vol. XIV, 1902-03, p. 492).

" 81. *Papilio polytes*, L. Common all over the district, especially around lime trees on which the caterpillar (which is very like that of *P. erithonius*) feeds. The species is on the wing throughout the rains and cold weather, the males, as a rule, appearing somewhat later than the females. Of the three forms of the latter, type I, which is like the male, does not apparently occur in the district; at any rate I have never seen it. Type II, which mimics *P. aristolochiæ*, is common and the only one generally taken; while type III, mimicking *P. hector*, is very rare, but as I have seen it on two occasions, apparently does occur. Its appearance at all is rather surprising as its model is never, as far as I know, found in Upper India."

Fatehgarh. H. D. Peile. (Vol. XX, 1911, p. 874).

" 22. *Papilio polytes*—Common '*cyrus*' form, two males taken. One '*romulus*' female taken, another seen"; *cyrus* is the male-like female form. If the two specimens were males the correct name would be *polytes*.

Kumaon. F. Hannyngton, I.C.S. (Vol. XX, 1910, p. 361).

" 168. *Papilio polytes*, L. Common up to 5,000 feet, May-November. I have not yet come across the *sakontala* form while the *romulus* form of the female seems to occur only in the Terai." By *sakontala* the author almost certainly means the male-like *cyrus* female form, *P. sakontala* being similar to the male *polytes*.

Masuri and neighbouring Regions. Philip W. Mackinnon, and Lionel de Niceville. (Vol. XI, 1897-98, p. 593).

" 258. *Papilio* (*Laertias*) *polytes*, L. Very common in the low valleys near Mussoorie from April to October and in the Dun almost throughout the year. The females are of three forms."

Sikkim. Lord Rothschild. (*Novitates Zoologicæ*, Vol. II, 1895. p. 347).

Refers to " Two speciments (of the *romulus* f.) in the Möller collection from Sikkim, one of which has the white of the forewings much less conspicuously marked and comes in the colour of these wings indeed close to certain specimens of female f. *polytes*; in the same example the red spot in the cell of the hind-wings is tinged with orange."

Darjiling District. C. M. Inglis (in a letter of 1st November 1920 to Prof. Poulton).

In the Darjiling district at Riang, elevation 2,000 feet, the following were taken by Mr. Shaw and seen and noted down by Mr. C. M. Inglis : males 5 ; *cyrus* female 1 ; *polytes* female 2 ; *romulus* female 1. Also at Mangpu, 3,860 feet :—males 2 ; *cyrus* 1 ; *polytes* 1.

Naga Hills. Major H. C. Tytler. (Vol. XXI, 1911, p. 589).

"205. *Papilio polytes*, L. Common at the foot of the hills throughout the year and a few at 4,000 feet in July and August ; the female form *cyrus* Fabr., is decidedly rare."

"194. *P. aristolochiæ*, Fabr. A few specimens taken at the foot of the hills in July and August and December."

Chin-Lushai expedition, 1889-90. E. Y. Watson. (Vol. VI, 1891, p. 53).

Papilio polytes, L. Pank, September ; Pokoko, October ; Pank to Tilin, November ; Tilin, December to May.

North Chin Hills and Upper Chindwin District. E. Y. Watson. (Vol. X, 1895-97, p. 672).

243. *Papilio* (*Laertias*) *polytes,* L. Common, but not noticed above 3,500 feet.

Tharrawaddy and the Pegu Yoma. E. V. Ellis. (Vol. XXV, 1917, p. 111).

"118. *P. polytes romulus*, Cr. Common, but I have only found the *polytes* form of female as yet.

"112. *P. aristolochiæ,* Fabr. The race *goniopettis,* Roth., is common every where, and it is the commonest *Papilio of* the district." *P. aristolochiæ goniopettis*, Rothsch., is the geographical race inhabiting Burma, Tenasserim and Siam northward to Hong Kong (*Nov. Zool.* XV, 1908, p. 167).

Tavoy. O. C. Ollenbach (in a letter of September 1919, to Prof. Poulton).

"Last February I visited Tavoy in Burma and while collecting for a few days I saw plenty of *P. polytes*, but no example of the *romulus* female."

This last observation was confirmed on 10th March 1920, when Mr. Ollenbach wrote, on his return from a collecting tour in the Tavoy district, " I took note of *P. polytes* and found only two kinds of female, the male-like and the *polytes* forms ; *romulus* was not seen."

Amoy. L. de Niceville. (Vol. XIII, 1900-01, p. 703).

"Of Insects, the butterflies were represented by one forlorn *P. polytes*, L., a damaged *P. clytia*,........"

13

Report, p. 518.

Mimicry. By Professor E. B. POULTON, *F.R.S.*

Special attention was drawn to the relationship between birds and butterflies and to the examples of injuries actually *seen* to be inflicted by wild birds, and, in comparison, examples of injuries very commonly found in butterflies. Stress is to be laid on 'disabling injuries,' such as the loss of the whole of a wing, indicating that the insect had not escaped, but was abandoned after being mutilated. There is evidence to show that these injuries are especially characteristic of the great groups which supply the models for mimicry. The author pointed to the negative evidence derived from the examination of birds' stomachs, and exhibited pellets thrown up by birds after a meal of butterflies, showing how completely the nature of the food has been disguised. The author showed illustrations and specimens of a few cases of mimicry in temperate North American butterflies, and pointed out what he believed to have been the evolutionary history. If this history be correct, then it is impossible to explain the resemblance as due to the influence of environment, because recent invaders from the Old World into this region have caused the mimetic modification of indigenous species. According to theory of environment the invaders ought to have been modified instead of the residents.

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Field-Observations on the Enemies of Butterflies in Ceylon. By J. C. F. FRYER, M.A., F.E.S.; Fellow of Gonville and Caius College, Balfour Student in the University of Cambridge.*

ETHOLOGY (BIRDS AND BUTTERFLIES).

The subject of Birds and Butterflies in Ceylon has already been admirably dealt with by Col. N. Manders in his paper entitled "An Investigation into the Validity of Müllerian and other forms of Mimicry, with special reference to the Islands of Bourbon, Mauritius, and Ceylon" †. In spite of this, however, I venture to place on record a few further notes from the island, partly because they deal more fully with the butterfly-eating habits of a most interesting bird, the Wood-Swallow (*Artamus fuscus* Vieill.), but also because the subject, with its direct bearing on the various theories of mimicry, is essentially one which requires as many observations as possible before any fair generalisations can be made.

A residence of a year and nine months, largely devoted to entomological research, gave an opportunity for keeping a continual watch on certain of the more common insectivorous birds; and the following notes comprise every observation made during that period. The locality in each case, unless otherwise stated, is the celebrated Botanical Garden at Peradeniya ‡. Other localities mentioned are Vavonia-Valunkulam, Maha Illupalama, and Trincomalee—all places in the hot dry northern country, which is characterised by the large area of jungle it contains, and also, in my experience, by a greater quantity of butterflies and other insect life than can usually be found in the hills.

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* Communicated by Prof. J. STANLEY GARDINER, M.A., F.R.S., F.Z.S.
† Proc. Zool. Soc. 1911, p. 696.
‡ Elevation about 1600 feet.

The notes are given in chronological order, and are extracted from my journal practically without alteration, as this method, though possibly wearisome, places a check on the personal prejudices of the observer, the introduction of which it is difficult to avoid in a mere summary of results.

PERADENIYA.

1911. *April 7th.* A drongo* took a *Papilio polytes* Linn. ♂, which could hardly fly, as it had only just emerged; it then caught a *Melanitis ismene* Cram., also released soon after it had left the pupa.

April 2nd–9th. General note that "drongos were only observed to take small butterflies, chiefly *Yphthima ceylonica* Hewit., Lycænids, and occasionally *Precis iphita* Cram." "Of the various attempts quite one out of two missed their object, while in many cases the swoop at a butterfly seemed to be taken more for amusement than to gain food." "Paradise fly-catchers (*Terpsephone paradisi* Linn.) being more retiring, were harder to observe; they certainly took *Yphthima ceylonica* and small Lycænids, but were not observed to attack anything large." [This week, April 2nd–9th, was spent mainly in bird observations, and the above is the result.]

April 15th. A drongo was seen to attack *Catopsilia pyranthe* Linn., but apparently without success.

May 9th. A drongo was seen to take an *Yphthima ceylonica* in the garden. . . . Three drongos chased a *Papilio parinda* Moore, but did not catch it. . . . Two bulbuls (*Molpastes hæmorrhous* Gm.) chased an orange-coloured moth, probably *Argina* sp., but lost it.

June 25th. A Paradise fly-catcher swooped at a *Limenitis calidasa* Moore, which escaped.

July 9th. A magpie-robin (*Copsychus saularis* Linn.) took a specimen of the Chalcosiid moth, *Heterusia cingala* Moore †, and flew away with it.

October 16th. A drongo chased a *Papilio parinda*, but lost it.

October 19th. A drongo caught a *Papilio polytes* ♂, and ate it.

October 21st. A scanty *P.-polytes* migration for the last three days. . . . A drongo swooped at a *P. polytes* ♀ form *polytes* ‡, but missed it. Many females of the *romulus* form § with the entire hinder portion of the hind wings missing.

November 1st–15th (at Vavonia-Valunkulam). A continual migration of *Appias* (*A. paulina* Cram. and *A. albina* Boisd.),

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* Throughout, the word "drongo" is used for either *Dicrurus leucopygialis* Blyth, or *D. cærulescens* Linn. The former was more common; but the species in most cases was not ascertained.

† This should undoubtedly be an "inedible" species, as it has all the Chalcosiid's nauseous characters to a marked degree.

‡ *P. polytes* ♀ *polytes* resembles *Papilio aristolochiæ* Fabr.

§ *P. polytes* ♀ *romulus* resembles *Papilio hector* Linn. Both *P. aristolochiæ* and *P. hector* are common Ceylon insects.

Catopsilia (*C. crocale* Cram. with a few *C. pyranthe* Linn.), *Papilio polytes*, *P. jason* Linn., *P. nomius* Esper, and *P. hector* Linn. Bee-eaters (*Merops* sp.?) were common, but were only observed to chase butterflies (*P. jason*, *Appias* sp.) on three occasions, each attempt being unsuccessful. Wings of all the above butterflies were found occasionally along the roads, but not in any number.

November 25th (at Peradeniya). A drongo seen to take a *Papilio polytes* ♀ *romulus*, which was flying badly.

November 29th. A number of wings of *Euplœa* and *Danais* found on the ground in the garden. The only birds seen near were wood-swallows (*Artamus fuscus* Vieill.). The wings identified were:—*Euplœa core* Cram., fore wings 6; *E. kollari* Feld., fore wings 2; *E. coreta* God., fore wing 1; *Danais septentrionis* Butl., fore wings 5, hind wings 3.

November 30th. Spent an hour, 11 A.M.–12, watching the wood-swallows hawking butterflies, which appeared to be forming their sole food. The birds sat on the top branches of a leafless tree, and swooped out after their prey, usually effecting a capture. The successful attempts were estimated at two out of three. The butterfly was carried to the perch and the wings there discarded. Butterflies on migration were extremely abundant, and individuals of the genus *Catopsilia* were perhaps most numerous, though Euplœas, Danaids, *Papilio polytes* and *P. demoleus* Linn. were all quite common. The wood-swallows limited themselves almost entirely to Euplœas and Danaids, only three swoops at *Catopsilia* and one at *Papilio demoleus* being observed, and these were all failures. The majority of the discarded wings were blown into the river, but the following were collected, practically all of which must have fallen during the morning.

Result:—*Danais septentrionalis*: fore wings 61, hind wings 9.
Euplœa core: fore wings 48.
E. coreta: ,, ,, 29.
E. kollari: ,, ,, 6.
Euplœine hind wings 9, fragments 4.
Papilio demoleus: fragments 2.
P. polytes ♂ or ♀ *cyrus*-form *: fragments 7 (2 fore wings).
P. polytes ♀ *romulus*: fragments 5 (3 fore wings).
P. polytes ♀ *polytes*: hind wing 1.

The predominance of fore wings is explained by their greater weight, hind wings being blown further.

A pair of bee-eeters were feeding near the wood-swallows. Most of their attacks were on small insects; but four attempts on *Catopsilia* and two on *Papilio demoleus* were noted, all of which failed. These bee-eaters were either unskilful or only amused themselves with butterflies. A young Paradise flycatcher and a drongo confined themselves to small insects, in spite of the swarms of butterflies passing.

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* *Papilio polytes* ♀ *cyrus*-form resembles the ♂.

December 1st. Again visited the wood-swallows, but they left off feeding early; the butterfly migration was larger, with a higher percentage of *Euplœa.* It was distinctly observed in one case that the bird carried the butterfly, a *Danais septentrionis*, to its perch and then held it with its feet while it pulled the wings off with its beak[*]. Watched the bee-eaters again, and saw one attack first a *Papilio agamemnon* Linn. and then a *Euplœa*, but it missed each time. They were continually hawking small insects, which they presumably caught. No count could be made of discarded wings, as all had been blown by a high wind into the river.

December 2nd. Again watched the wood-swallows hunting. The butterfly was always carried back to the perch before the wings were removed, and it was noticed that portions of the wings were often left on and eaten. . . . After failing in a stoop, the birds rarely made another at the same insect. . . . Butterflies at some distance were usually taken, perhaps to allow the bird to attain greater pace. . . . If a butterfly noticed that it was being pursued, it at once dodged and, flying rapidly downwards, frequently escaped. Wings were again collected:—

Danais septentrionis: fore wings 35.
D. limniace: ,, ,, 4.
Euplœa core: ,, ,, 18.
E. coreta: one whole insect and fore wings 10.
E. kollari: fore wings 4.
Papilio polytes ♀ *romulus*: fore wing 1.

December 7th. Wood-swallows hunting in the afternoon; they usually stop before midday.

December 10th. A young Paradise flycatcher swooped at two *Papilio polytes*, a ♂ and a ♀ *polytes* form, which were flying round inside a large breeding-cage, but of course could not get at them.

December 16th. A drongo was seen to attack a *Papilio agamemnon* and snap off a portion of the hind wings. The butterfly escaped.

1912. *January 1st–6th* (at Maha Illupalama). Bee-eaters were very common and butterflies, notably of the genera *Catopsilia* and *Appias*, were abundant. The only attack observed was that of a bee-eater on a *Leptosia xiphia* Fabr., which was caught and eaten.

January 10th (at Peradeniya). A drongo caught a *Papilio polytes* ♀ *cyrus*-form, which had just emerged and had escaped from a breeding-cage.

February 22nd. A *Papilio polytes* ♀ *cyrus* escaped from a cage and was eaten by a drongo; it was flying very weakly, as one wing was broken halfway down the costa.

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[*] Legge, 'Birds of Ceylon,' vol. ii. p. 668, states that the wood-swallow beats off the wings of its prey.

March 6th. Noticed three wood-swallows sitting on the telephone-wires crossing the River Maha-Weliganga. They were hawking butterflies continually, and during the time they were watched selected species of *Euplœa* only from a passing migration which consisted largely of *Appias paulina.* A search for wings failed, as the birds confined themselves entirely to the river. The reason for this seemed to be that the butterflies were only caught with ease when away from cover; among vegetation they dodged their pursuers nine times out of ten. This fact was specially evident during this migration, as species of *Euplœa* and *Danais* were uncommon, and the birds were often forced to swoop at butterflies travelling along the river-bank instead of waiting for individuals to come out into the open.

March 8th. The migration of butterflies almost ended; but to obtain confirmation, by a fresh witness, of the fact that wood-swallows attack especially members of the genera *Euplœa* and *Danais*, Alexander * and I watched three wood-swallows for an hour, and we both plainly observed them eat over a dozen *Euplœa* and one *Danais.* We also saw one bird with a *Papilio*, either *P. polytes* ♀ *polytes* or *P. aristolochiæ*, but were unable to ascertain which. As before, the birds usually carried the butterfly in the beak, though occasionally it was transferred to the claws when the distance back to the perch was great.

March 15th. Watched the wood-swallows for three-quarters of an hour; *Appias* spp. common, *Euplœa* and *Danais* scarce. There were only two birds feeding, one probably young, for when the other caught a *Danais aglæa* Cram. the young one opened its beak and fluttered its wings as if asking for food, though it gained nothing by this proceeding. The old bird then ceased feeding, but the other, possibly encouraged by the sight of the *Danais*, worked steadily, soaring round in circles over the river. It caught five Euplœas out of seven attempts.

March 16th. Watched a wood-swallow for a quarter of an hour and saw it take two Euplœas.

March 17th. Watched a wood-swallow from 11.30–12. It took two Euplœas, but then seemed to have no room for more, as it sat for a long time with the abdomen of the last victim protruding from its mouth like a cigar.

March 18th. In five minutes saw two wood-swallows take three Euplœas and a *Papilio*, either *P. polytes* ♀ *polytes* or *P. aristolochiæ*, almost certainly the former.

March 22nd. Species of *Euplœa* and *Danais* abundant on migration. A wood-swallow picked out two Danaids (*D. limniace* and *D. septentrionis*) and then a *Euplœa*, after which it stopped feeding.

March 23rd. Watched the wood-swallows from 11.40 A.M.–12; two were under observation most of the time, occasionally four. They took six specimens of *Euplœa* and two *D. septentrionis.*

Mr. Alexander, Assistant Curator of the Perth Museum, W.A., to whom I am indebted for much critical assistance during his brief visit to the island.

April 23rd. A drongo swooped at and probably took either a *Papilio polytes* ♀ *polytes* or a *P. aristolochiæ.*

April 24th. Mr. Pole of Maskeliya[*] wrote that he saw two large dragonflies take two *Appias* sp. ? and one *P. polytes* ♂.

July 7th (at Maha Illupalama). Noticed the remains of *Danais septentrionis*, *Papilio jason*, *Appias paulina* and *A. albina*, killed probably by Asilid flies (*Scleropogon piceus* and other species), as the bodies were intact though empty. Asilid flies were twice seen carrying *Appias* sp. ? ♂.

August 8th (at Maha Illupalama). Caught an Asilid fly with a medium-sized dragonfly[†], which it was sucking through the eye, and later saw another Asilid killing a large *Cicada* ♂ which was flying madly about, shrieking (stridulating) all the time. A slight bite from an Asilid was most painful, and felt as if poisonous matter had been injected.

August 13th (at Maha Illupalama). Noticed Asilid flies kill *Appias* sp. ? ♂ and *Papilio jason.*

August 28th (at Habarana, Maha Illupalama District). An Asilid attempted to kill the formidable Ceylon hornet, *Vespa cincta*, which, however, escaped.

August 31st (at Trincomalee). A few *Euplœa* wings were found scattered about Fort Ostenburg; they were probably dropped by wood-swallows, which were hawking round the inner harbour.

September 1st (Trincomalee). On the Nilavelli-Kuchivelli road bee-eaters were numerous. One was seen to catch an *Appias* sp., and wings of *Euplœa*, *P. jason*, and *Appias* spp. were occasionally found on the ground.

September 7th (at Peradeniya). Released an *Actias selene* ♂. It flew fairly well, but was soon snapped up by a drongo, which, before eating it, first pulled off the "tails" and then the rest of the wings.

The observations having now been given at length, it is perhaps permissible to summarise the impressions gained in their making:—

i. Butterflies do not form any large percentage of the food of the more common insectivorous birds in Ceylon.
ii. With the exception of the Wood-Swallow, birds are by no means clever in capturing butterflies.
iii. The Wood-Swallow is the only bird which actually lives on butterflies, and it almost always chooses butterflies of the so-called nauseous genera *Danais* and *Euplœa*; it seemed, however, that this preference was due to the difficulty of catching faster-flying butterflies, and not to the superior flavour of the *Danais* or *Euplœa*.

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[*] Hill district, elevation about 4000 feet.

[†] This and one or two subsequent notes, though not dealing with butterflies, are included, as they seem worthy of record and yet are insufficient for a separate contribution.

iv. The various species of Bee-eaters, when attacking butterflies, usually choose members of the Papilionidæ and Pieridæ.

v. The Asilid diptera are formidable enemies to all other living insects. They are, however, present in large numbers only in the northern country, and then only for a limited period of the year.

vi. In Ceylon a resemblance to the genera *Danais* and *Euplœa* is doubtfully of value; in fact, in the neighbourhood of Wood-Swallows it is a distinct danger.

vii. The mimetic females of *Papilio polytes* are not obviously protected by their mimicry, and as a whole probably suffer about as much, or as little, from the attacks of birds as any other fast-flying butterfly in Ceylon.

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British Association for the Advancement of Science. Report, p. 199.

SECTION D: BOURNEMOUTH, 1919.

ADDRESS

TO THE

ZOOLOGICAL SECTION

BY

Dr. F. A. DIXEY, M.A., F.R.S.,

PRESIDENT OF THE SECTION.

One of the results of the great war now happily at an end has been its effect upon science. On the one hand it has checked the progress of scientific investigation; it has done much to destroy international co-operation and sympathy; it has removed from our ranks, temporarily or permanently, many admirable workers. On the other hand it has acted as a great stimulus in many departments of scientific inquiry, and it has given the general public an interest in many scientific questions which have hitherto met with little recognition or encouragement from the people at large. It was perhaps inevitable, but at the same time, as I venture to think, rather to be deplored, that that interest has tended to concentrate itself upon applied more than upon abstract science; that it has been concerned chiefly with the employment of natural knowledge in devising and perfecting new methods of destruction. Terrible as is the power which the present-day engines of warfare have attained, it may be reasonable to hope that some compensation for the mischief and suffering which they have caused may eventually be found in peaceful directions; that the submarine, the air-craft, and even the high explosive may cease to be a terror to civilisation, and in spite of their past history may after all become agents in the advancement of the general welfare :

> Hoc paces habuere bonae, ventique secundi,

will, let us hope, be a legitimate reflection in later times. But for the true scientific worker, I think I may safely assert, the primary object of his studies is the attainment of knowledge for its own sake : applications of such knowledge may be trusted to follow; some beneficial, some perhaps the reverse. Still, whether they do or do not so follow is less a concern of the scientific man than whether his labours have resulted in a fresh advance into the realms of the unknown. I confess to some sympathy with the feeling which is said to be expressed in the regular toast of a certain scientific gathering :—'Pure mathematics, and may they never be of any use to anybody.'

For genuine enthusiasm in the cause of science for its own sake, I think that we zoologists may claim a good record. We are by no means unmindful of the great benefits to humanity which have taken their rise more or less directly from zoological science. I need do no more than mention the services to medicine, great at the present and destined to be greater still in the future, that are being rendered by the protozoologist and the entomologist. We may look forward also to results of the highest practical importance from the investigations into the laws of heredity in which we are engaged with the co-operation of our allies the botanists. But what we are entitled to protest against is the temper of mind which values science only for the material benefits that may be got from it; and what above all we should like to see is a greater respect on the part of the public for science purely as science, a higher appreciation of the labours of scientific men, and a greater readiness, in matters where science touches on the common affairs of life, to be guided by the accumulated knowledge and experience of those who have made such matters the subject of constant and devoted study. If the war leads to any repair of the general deficiency in these respects, it will to that extent have conferred a benefit on the community.

Regarding, as I do, my present position in this Section as a great honour and privilege, especially in view of this being the first meeting of the British Association to be held after the war, I hope I may be allowed a few preliminary remarks of a somewhat autobiographical character. As far back as I can remember, zoology has been a passion with me. I was brought up in a non-zoological environment, and for the first few years of my life my only knowledge of the subject was gained from an odd volume of Chambers's 'Information for the People.' But on being asked by a visitor what I intended to do with myself when I grew up, I can distinctly remember answering, with the confident assurance of seven or eight, 'Zoology suits me best'—pronouncing the word, which I had only seen and never heard, as *zoo*logy. By the time I went to school, my opportunities had increased, but I soon found myself engaged in the classical and mathematical routine from which in those days there was little chance of escape. In due course I went to the University with a classical scholarship, which necessitated for the time an even more rigid exclusion of scientific aspirations than before. I mention this because I wish to pay a tribute of gratitude to the College authorities of that day, to whose wise policy I owe it that I was eventually able to fulfil in some measure my desire for natural, and especially biological, knowledge. After two years of more or less successful application to the literary studies of the University, I petitioned to be allowed to read for the final school in natural science. The petition was granted; my scholarship was not taken away, and was even prolonged to the end of my fifth year. This I think was an enlightened measure, remarkable for the time, more than forty years ago, when it was adopted. I only hope that we have not in this respect fallen back from the standard of our predecessors. The avidity with which I took up the study of elementary chemistry and physics, and the enthusiasm with which I started on comparative anatomy under the auspices of George Rolleston are among the most pleasant recollections of my youth. But from the force of circumstances, though always at heart a zoologist, I have never been in a position to give myself unreservedly to that department of biology; and even now, in what I must call my old age, I fear I cannot regard myself as much more than a zoological amateur. My working hours are largely taken up with serving tables.

What moral do I draw from this brief recital? Not by any means that I should have been allowed to escape a grounding in the elements of a literary education, though I think it quite possible that the past, and even the present methods of school instruction are not ideally the best. My experience has led me to conclude that much of the time spent over the minutiae of Greek and Latin grammar might, in the case of the average boy, be better employed. But I do not agree that a moderate knowledge of the classics, well taught by a sensible master, is useless from any reasonable point of view. To those of my hearers who appreciate Kipling, I would call to mind the vividly truthful sketch of school life called 'Regulus.' Let them reflect how the wonderful workmanship of the inspired and inspiring Ode of Horace, round which the sketch is written, must have sunk into the mind of the apparently careless and exasperating 'Beetle,' the 'egregious Beetle' as King calls him, to bear such marvellous fruit in after years. Beetle, as we all know, is no professional scholar, no classical pedant, but a man of the world who has not forgotten his Horace, and upon whose extraordinary literary skill those early school-tasks must have had, whether consciously or not, a dominating influence. How else could he have written 'Regulus'? 'You see,' says King, 'that some of it sticks.' So it does, if it is only given a fair chance; and in the skirmish between King the classical and Hartopp the science master, both right up to a point and both wrong beyond it, I give on the whole the palm to King. To revert to my own case. I do not regret a word of either the Latin or the Greek that I was obliged to read, nor even the inkling of the niceties of scholarship to which I got, I hope, a fair introduction. But I do think that I might have been allowed to start on scientific work at an earlier period, and that a good deal of the time spent, say, on Greek and Latin prose and verse writing, might in my case have been well spared for other objects.

To generalise what I have been saying. Start teaching your boy or girl on a good wide basis. Nothing is better for this than the old school subjects of classics, history and mathematics, with the addition of natural science. In course of time a bent will declare itself. Encourage this, even at the expense of other studies desirable in themselves. But do not allow any one subject, however congenial, to usurp the place of a grounding in those matters which are proper to a general education. The time for specialising will come; and when it has arrived do all you can to remove obstacles, pecuniary and other. Do not hamper your historian with chemistry or your zoologist with the differential calculus. If they have a taste for these things by way of diversion or recreation, well and good. But let their action be voluntary.

This, however, is not a fitting occasion for propounding my views on the question of education, and it is time to turn to the immediate object of my address. And here I think I cannot do better than to bring before your notice certain facts which have a bearing on the subject of insect mimicry; a subject which for many years past has engaged much of my attention. The facts on all hands are allowed to be remarkable. As to their interpretation there is much diversity of opinion; and indeed, until complete data are forthcoming, this could hardly be otherwise.

In the first place let us glance at a certain assemblage of butterflies that inhabits New Guinea with some of the adjacent islands. These butterflies, though belonging to different subfamilies, present a resemblance to each other which is too strong to be accidental. Three of them belong to the Pierines, the group which includes the common white butterflies of this country; the fourth is a Nymphaline, not widely removed from our well-known tortoiseshells, red admiral and peacock. The resemblance on the upper surface between two of the three Pierines is not especially noteworthy, inasmuch as they present in common the ordinary Pierine appearance of a white or nearly white ground colour with a dark border somewhat broadened at the apex. But this, an everyday feature in the Pierines, is almost unknown in the very large subfamily to which our present Nymphaline belongs. Still, though sufficiently remarkable to arrest the attention of anyone familiar with these groups, the Pierine-like aspect of the upper surface of this Nymphaline, which is known as *Mynes doryca*, would not by itself have seemed to call for any special explanation. The resemblance would pass as merely an interesting coincidence. But the under surface of the three Pierines, known respectively as *Huphina abnormis*, *Delias ornytion* and *Delias irma*, presents a striking combination of colour very unusual in their own group; and this peculiar character of the under surface is shared by the Nymphaline *Mynes doryca*. The 'long arm of coincidence' could scarcely reach as far as this. Whatever might be said about the likeness seen from above, that the wings beneath should show virtually the same unusual pattern in the *Mynes* as in the Pierines seems to call for some explanation other than an appeal to chance or accident. Moreover, with regard to the Pierines themselves, the two members of the genus *Delias* are of course fairly closely related; but the *Huphina* belongs to an entirely distinct genus, separated from *Delias* by many important structural differences. The two species of *Delias* perhaps depart less widely in aspect from their nearest congeners than does either the *Huphina* or the *Mynes*. The under surface of the *Huphina* is unexampled in its genus, but the upper surface is quite ordinary. The *Mynes*, as we have seen, stands alone among its nearest relatives not only in the character of its under surface, but also in the Pierine-like character of its wings above.

We will now turn to another assemblage, which presents us with the same problem from a somewhat different point of view. In south-eastern Asia, with certain of the adjacent islands, is found a genus of large butterflies, called by Wallace *Prioneris* from the saw-like front margin of the forewing in the male. More than fifty years ago it was remarked by Wallace that the species of *Prioneris* in several cases seem to mimic those of the genus *Delias*, and that 'in all cases the pairs which resemble each other inhabit the same district, and very often are known to come from the same locality.' The parallelism is even stronger than was stated by Wallace, for there is not a single known member of the genus *Prioneris* which does not resemble a species of *Delias*, so that *Prioneris* cannot really be said to have an aspect of its own. *Prioneris clemanthe* and *Delias agostina* form a pair inhabiting the Himalayas, Burma and Further India. In the same region occur *Prioneris thestylis* and *Delias belladonna*, the striking similarity of which species, especially on the underside and in the female, drew the special attention of Mr. Wallace. A still more remarkable instance is that of *Prioneris sita* of southern India and Ceylon, the likeness of which to the common Indian *Delias eucharis* is spoken of by Wallace as 'perfect'; while Fruhstorfer, a hostile witness, testifies to the fact that the *Prioneris* always flies in company with the *Delias*, and rests just like the latter with closed wings on the red flowers of the Lantana. *Prioneris hypsipyle* of Sumatra and *P. autothisbe* of Java are like *Delias egialea* and *D. crithoe* of the same two islands. Here again Fruhstorfer says of *Prioneris autothisbe*, that it visits the flowers of the Cinchona, 'always in company with the similarly coloured *Delias crithoe*.' Wallace remarked on the close similarity between *Prioneris cornelia* of Borneo and *Delias singhapura* of the Malay Peninsula; in this case, it will be noted, the localities though not far distant from each other, are not identical. But a *Delias* form which was unknown at the date of Wallace's paper has since been found in Borneo, and this latter butterfly, known as *D. indistincta*, is even more exactly copied by *P. cornelia* than is the *Delias* which first drew Wallace's attention. *Prioneris vollenhorii* of Borneo is a kind of compromise between *Delias indistincta* and, on the underside, *D. pandemia* of the same island, and it may be added that another Bornean Pierine, *Huphina pactolica*, is a good copy of *Delias indistincta*, therefore resembling also the Bornean *Prioneris cornelia* and *P. vollenhorii*.

The memoir, published in 1867, in which Wallace remarked on the parallelism between *Prioneris* and *Delias*, contains a noteworthy prediction by the same author. Speaking of *Pieris* (now called *Huphina*) *laeta* of Timor he says that it 'departs so much from the style of colouring of its allies and approaches so nearly to that of *Thyca* (*Delias*) *belisama* of Java, that I should almost look for an ally of the last species to be discovered in Timor to serve as its pattern.' Thirty-four years after the expression of this anticipation, Mr. Doherty discovered in Timor an ally of *Delias belisama* which at once suggests itself as the model from which the peculiar and brilliant colouring of *Huphina laeta* has been derived. Fruhstorfer, who is by no means friendly to the theory of mimicry, says of this *Delias*, which was named *splendida* by Lord Rothschild, that beneath it is 'deceptively like *Huphina laeta*.' But here comes in a curious point. The black forewing with its yellow apex and the orange-yellow hindwing with its scarlet black-bordered costal streak are present on the underside of both the *Delias* and the *Huphina*; but the latter butterfly possesses in addition to these features a row of scarlet marginal spots on the hindwing which are not to be found on the *Delias*. In spite of this discrepancy, the likeness is sufficiently striking. But from the same island of Timor, Doherty sent home another *Delias* which besides resembling *D. splendida*, possesses a row of scarlet patches in the corresponding situation to those of *H. laeta*. In this latter *Delias*, however, named *dohertyi* by Lord Rothschild after its discoverer, the brilliant scarlet costal streak is completely absent. The *Huphina*, therefore, is more like either species of *Delias* than they are like each other, forming, as it were, a link between them. So that, adopting Professor Poulton's terminology, we may say that, if this is a case of mimicry, one form may possess at the same time the aposemes belonging to two distinct models. I will not now stop to discuss the bearing of this case on current theories, but will only remark that, granting mimicry, the whole assemblage, *D. splendida*, *H. laeta*, *D. dohertyi*, may be expected to gain advantage from the blending action of the intermediate *H. laeta*. This I think would happen whether *laeta* is a 'Batesian' or 'Müllerian' mimic, but the gain to the association in the latter case is certainly the more obvious.

This state of things would be sufficiently curious if it stood by itself. But it does not stand by itself. In Lombok, Sumbawa and Flores there occurs another member of the peculiar group of *Huphina* to which *H. laeta* belongs. This butterfly, known as *H. temena*, resembles *H. laeta* in many respects; possessing on the underside of the hindwing a scarlet costal streak and a row of scarlet marginal spots like those of that insect. The forewing, however, differs from that of *H. laeta* in having its ground-colour not uniformly black, but divided between a dark shading to the veins, a dark submarginal band, and series of pale streaks and patches in the interspaces between the veins. The question at once suggests itself: Is there a relation between *H. temena* and one or more species of *Delias* corresponding to that between *H. laeta* and *D. splendida* and *dohertyi*? The answer to this question is in the affirmative. *Delias oraia*, together with *Delias sumbawana*, both species inhabiting the same three islands as *H. temena*, form with it an assemblage quite comparable with the former triad from Timor. Further, the points in which *H. temena* differs from *H. laeta* have their counterpart in the distinctions between *D. oraia* and *D. splendida* on the one hand, and *D. sumbawana* and *D. dohertyi* on the other. These points are chiefly, in the *temena* assemblage, the less definitely black-bordered costal streak, the more strongly-marked black bordering to the submarginal scarlet spots, and the diversely-coloured as compared with the uniformly black forewing of the Timor insects.

Again, in the island of Bali, *Huphina tamar* would seem to combine certain features of two species of *Delias* in a similar manner to the cases of *laeta* and *temena* just considered. The underside as a whole is reminiscent of *D. periboea*, a member, like *D. dohertyi* and *D. sumbawana*, of the *eucharis* or *hyparete* group of the genus; while the red costal streak suggests the influence of a representative in Bali of the *belisama* group, like *D. splendida* and *D. oraia* in the other islands.

Finally, in the island of Sumba we have another member of this remarkable group of *Huphinas*. *Huphina julia*, the butterfly referred to, so closely resembles *Delias fasciata* of the same island, that even the sceptical Fruhstorfer is constrained to speak of it as a 'faithful copy' of that insect. But here once more it is noticeable that one of the most conspicuous features of the *Huphina* is absent from the *Delias*. This time it is not, as in the case of *D. splendida*, the submarginal row of scarlet spots on the underside of the hindwing, but it is the scarlet costal streak that is wanting. *Huphina julia* was discovered by Mr. Doherty in the year 1887, and described in 1891. It is interesting, in the light of what is now known of the butterfly fauna of the Lesser Sunda islands, to read what Doherty has to say about the mimicry question in relation to the *Delias* and *Huphina* forms that have just been mentioned. Speaking of *H. julia*, he says, 'If it stood alone, I should certainly suppose it to be a mimic of some form of *Delias hyparete* yet undiscovered in the island. But both *H. laeta* and *H. temena* require to be accounted for in the same way, and while it is possible that some Timorese *Delias* may resemble *H. laeta*, I feel sure that *H. temena* can have no such original. It must then be assumed that this group is less pressed by its enemies in the Timorian Islands, and has therefore been able to acquire more brilliant colours than its allies.' So far Doherty.

Whatever may be the value of this last hypothesis, we have just seen that the supposed facts on which it rests are non-existent, for (1) the 'form of *Delias hyparete* as yet undiscovered' has actually turned up in the person of *D. fasciata*; (2) it is not only possible, but actually the case that 'some Timorese *Delias* may resemble *H. laeta*'; (3) Mr. Doherty 'feels sure that *H. temena* can have no such original,' but *Delias oraia* and *Delias sumbawana* have just the same relation to *Huphina temena* as *D. splendida* and *D. dohertyi* to *H. laeta*. In view of these facts it may be not rash to suppose that the apparent absence of a model for the red costal streak of *H. julia* may hereafter be accounted for.

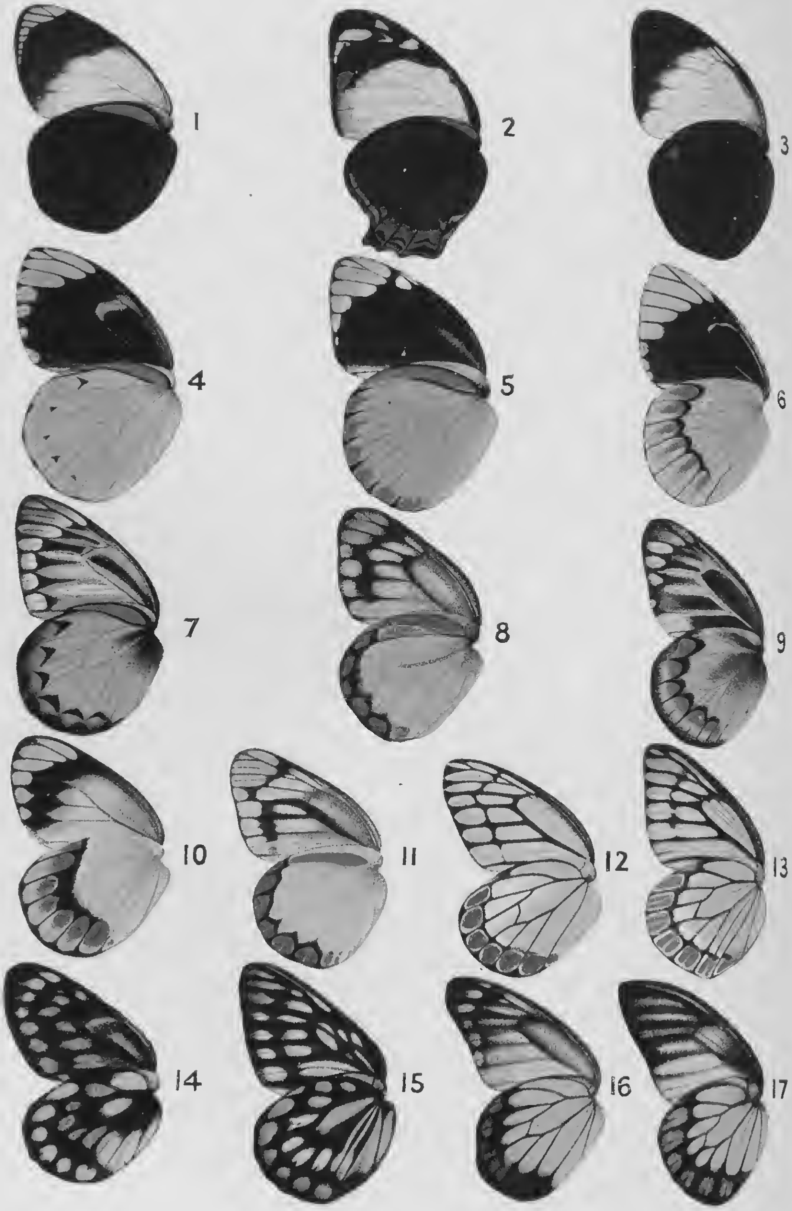
Of the three instances of possible mimetic association which have now been mentioned, I think that only one—*viz.*, the first, has previously been treated in detail. The numbers of cases more or less similar to these three might be very largely extended, but for our present purpose it will be sufficient to confine our attention to those already given. It is probable that to some minds the facts adduced are simply curious coincidences, needing no explanation; but it can hardly be wrong to suppose that to most students of nature the observed phenomena do call for some attempt at interpretation; and on a review of the evidence it seems clear that the geographical element must enter largely into any explanation that may be offered. On the whole, it is certainly the case that the forms which are supposed to be related by mimicry do inhabit the same localities; the continental *Prioneris*, for example, is like the continental *Delias*, and the island *Prioneris* recalls the island, not the continental, *Delias*. Moreover, we find the differences between the *Delias* of Timor, of Sumbawa and Sumba, reflected in the associated *Huphinas* of the same islands. If it be granted that the geographical element is a factor, it is natural to inquire how it works.

It is no doubt true that external geographical conditions are occasionally capable of producing, whether directly or indirectly, a community of aspect in the animals or plants exposed to their influence. The prevalence of a sandy coloration in the mammals and birds of a desert, and of whiteness in the inhabitants of the arctic snow-fields, the spiny character so often assumed by the plants of arid regions, and the general dwarfing of the vegetation that grows close to the sea, may be given in illustration. At first sight these phenomena may seem to be of the nature of direct effects of the environment; quite possibly some of them are so, but I think that few observers would deny that they are at least largely adaptive, being used for purposes of aggression or defence. Still, even if we allow the direct effect of the environment, as perhaps we may do especially in the case of the plants, can we frame any hypothesis of the action of geographical conditions which shall lead directly to the assumption of a common pattern in the case of the three or four butterflies from New Guinea? I confess that I am quite unable to do so. If the climate, or the soil, or any other geographical condition in New Guinea is capable of directly inducing so remarkable a combination of colour as we see in these Pierines and Nymphaline, why does it not affect other organisms in a similar way? Why do not other Pierines, for instance, closely related to *ornytion* and *abnormis*, share in the same coloration? And considering the characteristic aspect of the underside, which is supposed to be called into being by some unexplained condition peculiar to New Guinea, we may well ask, Why should its most conspicuous features belong in the one case to the forewing and in the other to the hindwing, and *vice versâ*, the general effect being the same?

Fruhstorfer, we may note, does not feel these difficulties. 'Many Pierids,' he says, 'present typical examples of that resemblance to other butterflies which has been named Mimicry. The origin of this resemblance, however, is now explained by the supposition that the mimics were modified by the same (as yet unknown) influences under which the colouring of the models, mostly Danaids, developed.' I think it will be generally agreed that this reference to 'unknown influences' is no explanation at all.

It is necessary to take into account the fact that the resemblances of which we are speaking are independent of structural differences, being, in fact, merely superficial. This is a point which is capable of much wider demonstration than I am giving it to-day. But even from the instances now before us I think there cannot be much difficulty in coming to the conclusion that the resemblances are an appeal to vision. They are meant to be *seen*, though by whom and for what purpose may be open to question. Speculations as to recognition and sexual attraction may, I think, in these cases be put out of court; but there remains the theory of warning colours assumed in reference to the attacks of vertebrate enemies. From the fact that the most striking and most conspicuous of these common aposemes or danger-signals belong to the under surface—that is to say, the part chiefly exposed to view during rest—it may be inferred that the enemies to be guarded against are mainly those that attack butterflies not on the wing, but when settled in repose. Both birds and monkeys are known to feed on butterflies, and there is a good deal of evidence as to their preference for one kind of food over another. I will not stop to give details, but anyone who wishes to study the evidence may be referred especially to the Memoirs of Dr. G. A. K. Marshall and Mr. C. F. M. Swynnerton.

If the warning-colour interpretation of these resemblances be the true one, we see at once why they are so largely independent of structure and affinity. Being meant to catch the eye, they ride rough-shod, so to speak, over incon-



Illustrating 'The Geographical Factor in Mimicry.'

[*Between pages* 204 *and* 205.

EXPLANATION OF PLATE.

Fig.		
1.	Delias ornytion *Godm. & Salv.*	New Guinea
2.	Mynes doryca *Butl.*	,,
3.	Huphina abnormis *Wallace*	,,
4.	Delias splendida *Roths.*	Timor
5.	Huphina laeta *Hew.*	,,
6.	Delias dohertyi *Roths.*	,,
7.	Delias oraia *Dohrt.*	Lombok, Sumbawa, Flores
8.	Huphina temena *Hew.*	,,
9.	Delias sumbawana *Roths.*	,,
10.	Delias fasciata *Roths.*	Sumba
11.	Huphina julia *Dohrt.*	,,
12.	Delias eucharis *Drury*	India, Ceylon
13.	Prioneris sita *Feld.*	S. India, Ceylon
14.	Delias belladonna *Fabr.*	N. India
15.	Prioneris thestylis *Doubl.*	,,
16.	Delias indistincta *Fruhst.*	Borneo
17.	Prioneris cornelia *Vollenh.*	,,

spicuous features, such as venation; nor do they respect more than the nature of things obliges them to do, the ties of blood-relationship. Then, again, it is obvious why they occur in the same and not widely different localities; in some instances, as we have seen, their bearers actually flying in company and frequenting the same flowers; for the common aspect, supposing it to be in any sense protective, would only take effect when the sharers in it were exposed to the attacks of the same body of enemies; that is to say, when they inhabited the same locality. And this would be equally true, whether the warning colours are shared between distasteful forms, or whether they are deceptively adopted by forms unprotected by inedibility;—whether, in Professor Poulton's terms, they are synaposematic or pseudaposematic. I do not enlarge upon this part of the question, or upon the theories which are known under the names of Bates and Müller respectively, because these theories have been fully dealt with elsewhere, and I think I may assume that they are familiar to the greater part of my hearers. But that mistaken ideas as to what is really *meant* by protection and mimicry still prevail in some quarters, is evident from certain remarks of Fruhstorfer in dealing with the genus *Prioneris* which we have just been discussing. 'Wallace,' he says, 'regards the "rarer" *Prioneris* as a mimetic form of the "commoner" *Delias*. But I cannot accept his view, since mimicry among the in all respects harmless Pierids appears no sort of protection, and properly speaking the smooth-margined *Delias* should rather copy the armed *Prioneris* if there is assumed to be mimicry at all.' If anyone has no better knowledge than this of what is meant by the theory of mimicry, it is not wonderful that he should consider the subject unworthy of serious attention.

The warning-colour theory, then, gives a rational explanation both of the superficial character of the resemblances and of the geographical factor in their occurrence. But it obviously involves the reality of natural selection; and it is here that some are disposed to part company with the upholders of the theory. I have already referred to the fact that much positive evidence now exists both that butterflies are eaten and that preferences on the part of their enemies exist between one kind and another. I will only remark in passing that the objector on this score sometimes adopts an attitude which is scarcely reasonable, and which perhaps on that very account is somewhat hard to combat. The kind of objector that I mean begins by saying that the destruction of butterflies by birds and other enemies is not sufficient to give play for the operation of selection. You beg his pardon, and produce evidence of considerable butterfly destruction. To which he replies, 'O, they *are* eaten, are they? I thought you said they were protected.' This is a good dilemma, but the dilemma is notoriously an unconvincing form of argument. If a reply be called for it may be given like this: 'Butterflies are either preyed upon or they are not. If they are, an opening is given for selection; if they are not, it shows the existence of some form of protection.' The essence of the matter is that both the likes and dislikes of insectivorous animals, and the means of protection enjoyed by their prey, are not absolute but relative. A bird that will reject an insect under some circumstances will capture it under some others; it will, for instance, avoid insect 'A' if it can get insect 'B,' but will feed on 'A' if nothing else is to be had; and it is probable that hardly any insect is entirely proof against the attack of every kind of enemy. The relative nature of protection is readily admitted when the question is not one of mimicry or of warning colours, but of protective resemblance to inanimate objects. All degrees of disguise, from the rudimentary to the almost perfect, are employed; the lower degrees are allowed to be of some service, and on the other hand a disguise that is almost completely deceptive may at times be penetrated. This consideration applies also to the objection that the first beginnings of mimetic assimilation can have no selective value. If the rough resemblance to an inanimate object affords some amount of protection, though that amount may be relatively small, why should not the same apply to the first suggestion on the part of a mimic of an approach to the aposeme or warning colour of its model? The position that neither kind of assimilation is of service is intelligible, though not common; but there is no reason why benefit should be affirmed in the one case and denied in the other. There are further considerations which tend to deprive this latter criticism of force; the fact, for instance, that a resemblance to one form may serve as a stepping-stone for a likeness to another; or, again, the existence of clusters, as they may be called, of forms varying in affinity, but embodying a transition by easy stages from one extreme to another. In a case of this sort the objection that may be felt as to two terms in the series arbitrarily or accidentally picked out is seen to be groundless when the whole assemblage is taken together.

Much attention has lately been given to the fact that of individual variations some are transmissible by heredity and some are not; under the latter heading would generally fall somatic modifications directly induced upon the individual by conditions of environment. Whether any other kind of variation belongs to the same category need not for the present purpose come into discussion. But with regard to the undoubtedly transmissible variations, or mutations if we like to call them so, there is, I think, a fairly general consensus of opinion that they need not necessarily be large in amount. A complete gradation in fact appears to exist between a departure from type so slight as to be scarcely noticeable and one so striking as to rank as a sport or a monstrosity. And we know now that where the Mendelian relation exists between two forms, no amount of interbreeding will abolish either type; intermediates, if formed, are not permanent, and if one type is to prevail over the other it must be by means of selection, either natural or artificial.

In view of all these considerations I venture to think that there is no reason to dispute the influence of natural selection in the production of these remarkable resemblances. Other interpretations may no doubt be given, but they involve the ignoring of some one or more of the facts. It may fairly be claimed that the theories of Wallace, Bates and Müller, depending as they do on a basis of both observation and experiment, come nearer to accounting for the facts than any other explanation as yet offered. It will of course always be possible to deny that any explanation is attainable, or to assert that we ought to be satisfied with the facts as we find them without attempting to unravel their causes. But such an attitude of mind is not scientific, and if carried into other matters would tend to deprive the study of nature of what to most of us is its principal charm. It is quite true that before the validity of any generalisation is accepted as finally and absolutely established, every opportunity should be taken of deductive verification. This has been fully recognised by the supporters of the theory of mimicry, and much has been done to test in this manner the various conclusions on which the theory rests. The verification is not complete, and perhaps never will be, but every successive step increases the probability of its truth; and probability, as Bishop Butler taught, is the guide of life. Meantime it is, one may say, the positive duty of everyone who has the opportunity, to fill up, so far as is in his power, the gaps that still exist in the chain of evidence. Here is an especially promising field for naturalists resident in tropical regions.

Before concluding this address, there are two points on which I should like to lay some special emphasis. One is the undesirability—I had almost said folly—of undervaluing any source of information, or any particular department of study, which does not come within the personal purview of the critic or commentator. 'I hold,' says Quiller-Couch, 'there is no surer sign of intellectual ill-breeding than to speak, even to feel, slightingly of any knowledge oneself does not happen to possess.' This is a temptation to which many of us are liable; and falls, I fear, are frequent. It was a matter of sincere regret to me to find one of my most valued scientific friends speaking publicly of the Odes of Horace as a subject comparatively devoid of interest. I can only confess my utter inability to sympathise with my friend's point of view. If he had merely said, 'excellent as those works may be, I have other things to do than to attend to them,' I could approve; but that is a different matter. The failing that I speak of is unfortunately by no means unknown among scientific men, and is perhaps rather specially prevalent when such subjects as those of my present address are in question. I can recall a very eminent man of science, no longer living, speaking with scarcely veiled scorn of those who occupied themselves with 'butterflies in cases.' This was in a Presidential Address to a Section of this Association. If so little respect is paid by a leader of science to work done in another part of the field, it is perhaps not to be wondered at that one of His Majesty's Judges should speak of the formation of a great collection of butterflies—a most valuable asset for bionomic research—as the 'gratification of an infantile taste.' This or that collector may be an unscientific person, but it would be easy to show that the study of insects in general, and of butterflies in particular, is one of the most efficient of the instruments in our hands for arriving at a solution of fundamental problems in biology.

My second and final point is this. I have not hesitated to affirm my conviction of the importance in evolution of the Darwinian doctrine of natural selection. This necessarily carries with it a belief in the existence and general prevalence of adaptation. I am willing to admit that at times too much exuberance may have been shown in the pursuit of what Aubrey Moore called 'the new teleology.' 'Men of science,' it has been said, 'like young colts in a fresh pasture, are apt to be exhilarated on being turned into a new field of inquiry; to go off at a hand-gallop, in total disregard of hedges and ditches, to lose sight of the real limitation of their inquiries, and to forget the extreme imperfection of what is really known.' This is not the utterance of some cold outside critic, but of a great exponent of scientific method—no other than Huxley himself. It may be true of some of the wilder speculations of Huxley's date. I am by no means sure that there is not truth in it as applied to some of the developments of a later time. But however wide of the mark our suggested explanations and hypotheses may be, the net result of all our inquiries, after the gradual pruning away of excrescences and superfluities, will be a real advance into the realms of the unknown. We may feel perfectly assured that the objections so far brought against our own interpretations are null and void, but we may yet have to give way in the light of further knowledge. 'Let us not smile too soon at the pranks of Puck among the critics; it is more prudent to move apart and feel gently whether that sleek nose with fair large ears, may not have been slipped upon our own shoulders.'[1]

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[1] Dowden.

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Report, p. 518.

The Geographical Relations of Mimicry.

By F. A. DIXEY, *M.D.*, *F.R.S.*

It is well known that certain definite schemes of colour and pattern in the wings of butterflies are characteristic of certain definite geographical regions. This is true not only of the region as a whole, but also, in many cases, of the smaller districts into which the given region may be divided, the colour and pattern undergoing a similar modification in all the members of the associated assemblage as one such district gives place to another.

Illustrations of this phenomenon are afforded by a well-known combination of red, black, and yellow Ithomiine, Heliconiine, Danaine, Nymphaline, and Pierine butterflies in Central and South America, and by a similar parallelism existing between local forms of the African genera *Mylothris* and *Phrissura*. The constituent members of these assemblages are often of very diverse affinities.

It is natural to seek for an explanation of these facts in the direction of a common influence exercised by the geographical environment. But in the special cases cited, to which many others might be added, this explanation is attended by such extreme difficulty as to be practically put out of court. The interpretation that at present holds the field is that which attributes these resemblances, with their correlated geographical modifications, to the action of mimicry, whether of the Batesian or Müllerian kind. This interpretation rationalises the geographical facts without resorting to the exceedingly difficult hypothesis of a direct influence by the geographical conditions.

If the interpretation under the theories of mimicry be accepted there still remain some anomalies to be accounted for. A few of these may be set down as mere coincidences, such as might be expected where the array of facts is so extensive; others are probably due to migration on the part of the insects themselves or of their enemies; while there is a residuum which no doubt points to the fact that somewhat similar schemes of colour and pattern may take independent origin in entirely distinct regions of the earth's surface, and may in each such situation become the common property of a Batesian or Müllerian mimetic assemblage.

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VI. *On Mimicry in certain Butterflies of New Guinea.*

By F. A. Dixey, M.A., M.D., F.R.S.

[Read March 6th, 1918.]

In Seitz's "Macrolepidoptera" (Indo-Australian Region; English Edition, p. 147) under the genus *Huphina*, Fruhstorfer speaks of *abnormis*, Wall., "*euryxanthe*," Honr., and "*ornythion*," Godm. & Salv., as related species. This passage contains two minor inaccuracies and one distinct error. Honrath's insect was named by him *euryxantha*. Oberthür afterwards spelt the name with a final *e*, in which he has been followed by other authors. Staudinger, however, in "Iris," and Grose Smith and Kirby in their "Rhopalocera Exotica" rightly give the original spelling. The second inaccuracy is in the name "*ornythion*," which was written by its authors *ornytion*.

These are trivial matters; of greater importance is the statement of affinity between *ornytion* and the other two species. Though it bears so striking a resemblance to *Huphina abnormis*, the relationship of *ornytion* to that butterfly is not close, for it belongs in fact, as shown by structural characters, to the very distinct genus *Delias*. Much confusion has prevailed with regard to all three butterflies now named, and it may be worth while to attempt to clear this up before proceeding to the actual subject of my paper.

In his well-known memoir on the Eastern *Pieridae*, published in 1867, Mr. Wallace described and figured under the name of *Tachyris abnormis* a remarkable Pierine from New Guinea.* He observes that in coloration "it bears a striking general resemblance to the beautiful nymphalideous butterfly, *Mynes Geoffroyi*, which inhabits the same country." The type specimen, which may still be seen in the National Collection, is a female; if Wallace had been acquainted with the male, he could scarcely have avoided noting that it does not possess the anal tuft of hairs which characterises the genus *Tachyris*. But the general appearance of his specimen seemed to him to indicate that it came nearest to such forms as *ada*, Cram., and *clavis*, Wall., and he therefore placed it tentatively in his genus *Tachyris* next after those species. In 1889 Messrs. Grose Smith and Kirby * figured both the upper and under side of the same form; Wallace's figure only showing the latter. On the plate in "Rhopalocera Exotica" the species appears under Wallace's name of *Tachyris abnormis*, but in the text and indices its genus is given as *Delias*. The figure is said to represent a male, but is really (like Wallace's) that of a female. The mistake as to sex was afterwards corrected by the authors.† In the same work, vol. ii, *Pierinae*, p. 17, *abnormis* is once more referred to the genus *Delias*, and is said to belong to the group of *D. ladas*, Grose Smith, and *D. ornytion*, Godm. & Salv. But in the note (*Ibid.*, p. 22) cited above, the authors add, "Herr von Mitis points out ('Iris,' vi, p. 114), that the four-branched subcostal nervure removes both *Abnormis* and *Euryxantha* from *Delias*." This is quite true; and *euryxantha*, which appears in the plate ("Rhop. Exot.," vol. ii, *Pierinae* ; *Delias*, vi, figs. 7, 8) as a *Delias*, is in the text called a *Tachyris*.

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* Trans. Ent. Soc. Lond., Series III, vol. iv, p. 368; Pl. VIII, fig. 5, ♀.

Honrath,‡ who described *euryxantha* as a variety of *abnormis*, expressed a doubt as to whether Grose Smith and Kirby's figure of *abnormis* represented a male as stated; he adds, however, that those authors in their text rightly placed *abnormis* in the genus *Delias*, "to which genus, instead of to *Tachyris*, Wallace, if he had known the male, would certainly have also assigned it." Staudinger § definitely pronounced Smith and Kirby's figure to be that of a female.

As a matter of fact, neither *abnormis* nor *euryxantha* is either a *Delias* or a *Tachyris*. So far as I am aware, the first author to perceive their true affinity was von Mitis,‖ who, as above stated, pointed out that their neuration was not that of *Delias*. Von Mitis himself places them in the neighbourhood of *judith*, *amalia*, *emma*, etc.; *i. e.* in the group named by Moore *Huphina*, though ranked by the former writer under the wide designation of *Pieris*.

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* "Rhopal. Exot.," vol. i, *Pierinae*, Pl. II, figs. 6, 7.

† *Ibid.* vol. ii, *Pierinae*, p. 22, *note*.

‡ Berl. Entom. Zeitschr., xxxvi, p. 435 (1892).

§ "Iris," vii, pp. 117, 118 (1894).

‖ *Ibid.* vi, pp. 113, 114 (1893).

While there is little doubt that *abnormis* and *euryxantha* are best referred to *Huphina*, it is also true that they appear to stand somewhat apart from other members of that genus. The genitalia of both species are of the *Huphina* type, but the valves differ slightly in shape from those of *H. agnata*, Gr. Smith, and *H. nerissa*, Fabr. The genitalia in *Delias* are quite different. The scent-scales of *H. abnormis* cannot easily be distinguished from those of *H. euryxantha*, if, indeed, they can be distinguished at all. They are of the *Huphina* type, though shorter and proportionately broader towards the apex than those of other species of the genus. The difference in neuration between *Huphina* and *Delias* is well known. The neuration of *abnormis* and *euryxantha* is that of the former genus. Von Mitis agrees with Honrath in attributing Wallace's mistake to the fact that he was only acquainted with the female. Staudinger * speaks of von Mitis as having shown that *abnormis* and *euryxantha* belong to the genus "*Pieris* (or *Appias*)"; but these forms have certainly no more to do with "*Appias*" than they have with *Tachyris*, nor did von Mitis suggest the contrary.

As already stated, there is little or no doubt that *abnormis* and *euryxantha*, whether they are distinct species, or whether, as thought by Honrath, von Mitis and Staudinger, forms of the same species, have their true affinity with the Pierines included in Moore's genus *Huphina*. This was correctly recognised by Mr. A. G. Butler † in his Revision of that genus. But while rightly placing them in *Huphina*, to which group they almost certainly belong, he associates with them in the same genus *ladas*, *ornytion* and *dohertyi*, adding the following comment: "I must confess that the fact of the last five species occurring together in New Guinea, in conjunction with the fact that similarly coloured species of the Nymphalid genus *Mynes* occur there, is very suspicious. I cannot help thinking that breeding experiments would tend greatly to reduce the number of these 'species' in both genera." Mr. Butler's suspicions that something was wrong were well founded; and it is quite probable that breeding experiments would show that *abnormis* and *euryxantha* are conspecific, as was supposed by Honrath, Staudinger and others. But along with a possible reduction in the number of species, what is really required in the five forms associated in the "Revision" is an increase in the number of genera. The first two forms of the five, viz. *euryxantha* and *abnormis*, belong, as we have seen, to *Huphina*; but *ladas* and *ornytion* are certainly members of the genus *Delias*. With regard to the fifth species, viz. *dohertyi*, there is a fresh complication. A *Pieris dohertyi* from Jobi and a *Delias dohertyi* from Timor were both described in 1894, the former by M. Oberthür, the latter by Lord Rothschild. Oberthür's description having been published in August, and Rothschild's in September, it would seem that the former has priority. I have never seen Oberthür's type, but from the description and figure I have no doubt that it is a *Delias*. Rothschild's *dohertyi* is certainly a *Delias*, and quite distinct from Oberthür's. In his Revision of the genus *Delias*,* Mr. Butler refers under *D. dohertyi* to Rothschild's description above mentioned, and also to Grose Smith and Kirby's figures in "Rhopal. Exot.," ii, *Delias*, Pl. IV (not Pl. VI, as Butler), figs. 7, 8, which represent Rothschild's type. He adds, "It is a curious thing that in the same year when the above was described M. Oberthür described a *Pieris Dohertyi* from New Guinea. The latter, however, appears to me to be allied to *P. ornytion* of Godman and Salvin, in which case it is not a *Delias* (although *P. ornytion* has erroneously been referred to this genus by von Mitis)." But, as we have seen, *ornytion is* a *Delias*, and if Mr. Butler is right, as I believe he is, in thinking that Oberthür's *dohertyi* is allied to *ornytion* (of which species it seems to be the representative in the Island of Jobi), we have two *dohertyi* in the same genus, Oberthür's being apparently the one that is entitled to stand; unless indeed Oberthür's *dohertyi* should turn out to be a mere synonym of *ornytion*; in which case I presume that Rothschild's would stand as the true *dohertyi*. This, however, is a question that I would fain leave in the hands of experts in nomenclature.

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* "Iris," vii, pp. 117, 118 (1894).

† Ann. Mag. Nat. Hist., 7th Series, vol. iii, p. 206 (1899). It may be noted that Mr. Butler's reference to Oberthür's "Études" should be to p. 6, not to p. 61.

Turning now to Fruhstorfer's treatment of these forms, we find that he ends his account of *Huphina* with the same five species as those to which Butler called attention in the passage above quoted, adding to them "*persephone*, Staud. (= *odyssia*, Frust. *i. l.*)." † His notice of this assemblage is no doubt based on the "Revision"; * and we have already seen that three of its members, viz. *ornytion, ladas* and *dohertyi* belong not to *Huphina* but to *Delias.* There remains *persephone,* Staud., from Waigiou. This form, as Fruhstorfer says, "was formerly only known in one defective male specimen, and described as *Delias.*" His figure, which appears in *loc. cit.*, Pl. 63 d, as *Huphina odyssia,* is indistinguishable from specimens of *ornytion* from the Arfak Mountains in N.W. and from Kapaur in W. New Guinea, on the underside of which forms the submarginal red line of the hind-wing is wanting, and the yellowish patch on the apex of the fore-wing may also be absent, as in the figure of "*odyssia.*" Staudinger † was no doubt right in placing *persephone* in the genus *Delias*; there was also some justification for his surmise that a larger number of specimens, perhaps from other localities, might show that *persephone* is a local form of *ornytion.* As we have seen, there is no assignable difference between the Waigiou form and specimens of *D. ornytion* from Western New Guinea. Staudinger speaks of *ornytion* as from S.W. New Guinea, but Godman and Salvin's specimens, including the type, were taken near Port Moresby. Even in these the submarginal red line was almost obsolete; in another specimen from Port Moresby it is entirely lacking, as in the type of *persephone.*

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* Ann. Mag. Nat. Hist., 6th Series, vol. xx, p. 153 (1897).

† Seitz, "Macrolepidoptera" (Indo-Australian Region), Engl. Ed., p. 147.

We may sum up as follows:—

Abnormis is not a *Tachyris* (as Wallace, and Grose Smith and Kirby in their plate); nor a *Delias* (as Grose Smith and Kirby in their text and indices, also Honrath); nor a "*Pieris* (*Appias*)" (as Staudinger); but a *Huphina* (as von Mitis,‡ Butler and Fruhstorfer).

Euryxantha (not *euryxanthe*) is not a *Delias* (as Honrath in his description and Grose Smith and Kirby in their plate §); nor a *Tachyris* (as the two latter authors in their text and indices); nor a "*Pieris* (*Appias*)" (as Staudinger); but a *Huphina* (as von Mitis, Butler and Fruhstorfer). It may probably be conspecific with *abnormis.*

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* The reference to Oberthür's Etudes, "p. 61" (instead of p. 6), above noted in the "Revision," is repeated in Fruhstorfer's Alphabetical List of Indo-Australian Pierines; *loc. cit.*, p. 185.

† "Iris," vii, p. 355 (1895).

‡ He calls it *Pieris,* but is aware of its true affinities.

§ Both *abnormis* and *euryxantha* are also assigned to *Delias* by Grose Smith in Novit. Zool., i, pp. 334, 335 (1894).

Ornytion (not *ornythion*), described as a *Pieris*, is not a *Huphina* (as Butler and Fruhstorfer); but a *Delias* (as Staudinger, von Mitis, and Grose Smith and Kirby).

Persephone is not a *Huphina* (as Fruhstorfer); but a *Delias* (as Staudinger).

Dohertyi, Oberth., described as a *Pieris*, is not a *Huphina* (as Butler and Fruhstorfer); but a *Delias*. The three last-named forms are very probably conspecific.

Dohertyi, Roths., is rightly assigned to *Delias* by its describer, by Grose Smith and Kirby, and also by Butler.

Ladas is not a *Huphina* (as Butler and Fruhstorfer); but a *Delias* (as Grose Smith and Kirby).

The confusion that has prevailed with regard to these species affords a good illustration of the way in which even skilled entomologists may be misled as to affinity by striking resemblances in colour and pattern. It is surely not unreasonable to suppose that analogous mistakes may be made by insectivorous enemies.

To turn now to the main subject of this paper. It will be observed that all the forms that have been mentioned are inhabitants of New Guinea and adjacent islands; also that, leaving *Huphina euryxantha* and the form of *Mynes geoffroyi* with a light hind-wing out of account, the remainder are characterised by a uniform dark coloration of the under surface of the hind-wing, in some cases relieved by streaks, touches or lines of bright red. The butterflies in question belong to three different genera; two of the genera, viz. *Delias* and *Huphina*, being included in the subfamily *Pierinae*, and the third, viz. *Mynes*, in the subfamily *Nymphalinae*. Of all these forms, *Delias ornytion* may perhaps be regarded as the most characteristic. I am not acquainted with the habits and postures of any of the members of this assemblage; but if *D. ornytion* behaves like most other Pierines, its attitude while feeding or resting during the intervals of flight would show on the underside a striking contrast between the dark hind-wing and apex of fore-wing on the one hand, and the white portion of the fore-wing on the other. The appearance of the butterfly, already conspicuous and distinctive, would be rendered still more so by the red costal streak and red patches or submarginal line of the hind-wing. *Huphina abnormis* under similar conditions would display the like contrast between white, blackish brown and scarlet, though here it is interesting to observe that on a close comparison the scarlet streak in *abnormis* is seen to be not, as in *ornytion*, on the costa of the hind-wing, but on that of the fore-wing. The thin scarlet submarginal line, often present in *ornytion*, is also absent from *abnormis*, though a suggestion of it may occur in the form of a few scarlet patches. *Mynes geoffroyi*, or rather the form *doryca*, would present, as was observed by Wallace, the same general appearance as *abnormis*, the contrasting colours being very nearly the same. But here the relative position of the scarlet touches is again somewhat different. Comparing *doryca* with *abnormis*, we see a rough correspondence between the scarlet costal streak on the hind-wing of the former and that on the fore-wing of the latter; also between the scarlet submarginal spot on the hind-wing of the latter and that on the fore-wing of the former. As in *abnormis*, so in *doryca*, the hind-wing has no scarlet submarginal line. The apex of the fore-wing is in *doryca* diversified with certain light-coloured marks; these are absent from *abnormis*, but many specimens of *ornytion* show a paler area, much less conspicuous than in *doryca*, but in the corresponding situation.

If these insects, after the usual manner of butterflies, depress the fore-wings during the periods of protracted rest, so as to conceal the white portion of the fore-wing and leave visible only the apex of the fore-wing and the whole expanse of the hind-wing, the resemblance between them becomes perhaps even more detailed. The costal and submarginal red marks fall more nearly into their right relative positions, irrespective of their situation on fore- or hind-wing; and the assemblage is now joined by another *Delias* from New Guinea, viz. *D. irma*, Fruhst. In the male of this butterfly the under surface of both wings is black, with the exception of a scarlet patch on the costa of the hind-wing, like that of *D. ornytion*, but somewhat shorter in proportion; there may also be a powdering of orange-yellow scales about the distal end of the cell in the fore-wing, though this is often evanescent or absent.

It is difficult to see how the facts with regard to these four insects can be interpreted without recourse to the theory of mimicry. The resemblance between two of them, as has been seen, has been sufficient to cause great confusion, even on the part of skilled entomologists; and it is hardly necessary to point out the improbability of this striking resemblance between insects differing in affinity, but all inhabiting the same region, being due to simple coincidence. Nor, again, is it easy to suppose any factor in the climate or external conditions of New Guinea which could lead directly, on the part of three or four of its butterflies, to the assumption of a dark underside with red markings; these markings, be it observed, belonging in some cases to the fore-wing, in others to the hind-wing, but always contributing to the same general effect. Whether the explanation founded on mimicry is adequate, can only be finally decided by observation and experiment; at present I think it must be admitted to hold the field.

The scarlet markings on the hind-wing underside of *Delias ornytion* would seem to be an attenuated version of the subcostal red patch and submarginal red band seen in the corresponding position on the hind-wing of *Delias harpalyce*, Donov., and *Delias nigrina*, Fabr. This series of markings has a wide distribution among the species of *Delias*, being more or less completely represented in such species as *D. aganippe*, Donov. (Australia); *D. kummeri*, Ribbe, *iltis*, Ribbe, and *bakeri*, Kenr. (New Guinea); *D. mysis*, Fabr. (Australia); *D. argenthona*, Fabr. (Australia); *D. caeneus*, Linn. (Moluccas); *D. eucharis*, Drury (India); *D. stolli*, Butl. (China); *D. eumolpe*, Gr. Smith (Borneo). A comparison of these and other forms appears to favour the conclusion that in *D. ornytion* we have the red submarginal series in an obsolescent rather than in an incipient stage; and it is observable that although the subcostal scarlet patch is persistent throughout the whole range of this species, the submarginal scarlet line, which is nearly always present in specimens from Eastern New Guinea, and is well marked in a specimen from the Louisiade Archipelago, has, in all the examples known to me from Western New Guinea and the adjacent islands, completely vanished without leaving a trace. Now it is to be remarked that the failure of the red line in *D. ornytion* brings its underside, with closed wings, into relation with that of *Delias inferna*, Butl. (or as Fruhstorfer calls it when it occurs in New Guinea, *D. irma*). On the mimetic hypothesis, it would be natural to ask whether the darkening of *inferna* has been influenced by *ornytion*, and the loss of red in *ornytion* by the condition in *inferna.* No doubt much remains to be discovered about the distribution of these forms in New Guinea, which is a very large country. But as far as is known at present, the disappearance of the red line of *D. ornytion* in the western part of its area cannot be connected with the presence of *D. inferna* or "*irma,*" for the latter form appears not to occur in the western half of the island. On the other hand, it would seem to be not impossible that the dark coloration of *inferna* as compared with the other members of the *aruna* group may have been influenced by *ornytion*; for the only region outside the range of the latter where *inferna* occurs appears to be the northern extremity of the Cape York peninsula.

It is doubtful whether any geographical relation can be traced in the case of the red spots of *Huphina abnormis.* The submarginal series of the hind-wing occurs in greater or less development in specimens from Eastern New Guinea, the first at least of the series being apparently always present. The type, which is entirely destitute of the hind-wing series, is said by Wallace to have come from "N.W. Papua"; but the present data are obviously insufficient for forming any conclusion on this head. Nor, again, can it be said that *Mynes doryca,* which is generally distributed throughout New Guinea, shows any difference in the development of its red spots in correspondence with locality.

The facts that can be affirmed with certainty are that these four forms, viz. *Delias ornytion, D. irma, Huphina abnormis* and *Mynes doryca,* all resemble each other, and depart from most of their congeners, in the possession of a dark, almost black under-surface to the hind-wing, on which occurs a series of red markings in a greater or less state of development; that in two of them (*Mynes* and *Huphina*) the red series is divided between fore- and hind-wing, but presents the same general appearance as in the two *Delias* in which it is to be seen on the hind-wing alone; and that in one of the four (*D. irma*) the under-surface of the fore- as well as of the hind-wing is dark, so that in the other three the attitude of complete rest (fore-wings depressed between hind-wings) must be adopted in order to produce resemblance to the first. Whether these facts are open to an interpretation on the basis of the theory of mimicry is a question which will be answered in different senses by different authorities; but to those who admit the validity of the theory in any form, it will seem probable that some mimetic influence at any rate has here been at work, though it may not be possible to determine its exact extent.

We have seen that there is little doubt that the markings on the hind-wing underside of *D. aganippe* are generally homologous with those in the corresponding situation of *D. nigrina*; and equally little doubt that the scarlet markings of *D. ornytion* are an attenuated version of the subcostal patch and red band or chain of spots seen in the two former and many other species of *Delias*, especially those belonging to what may be called the *eucharis* section of that genus. In Trans. Ent. Soc. Lond., 1894, pp. 300, 301, and Proc. Ent. Soc. Lond., 1909, p. cxiii, reasons were given, on the combined evidence of wing-markings and scent-scales, for supposing that the *eucharis* section is a natural group distinct from the *belisama* section, though no doubt at one time linked with it through a form more or less resembling *Delias aganippe*. *D. inferna*, which is a local race of *D. aruna*, Boisd., is shown by both kinds of evidence to be closely akin to *belisama*, and so to belong to an assemblage in which the red subcostal patch is nearly always present, and the red submarginal chain is as a rule not to be found.* It was therefore rather to be expected, on the theory of a mutual approach between *D. inferna* and *D. ornytion*, that the latter should be more apt to lose the already attenuated submarginal line than the former to revive it or start it afresh.

Two other points of interest in connection with this assemblage remain to be noticed.

(1) With regard to *Mynes doryca* it is to be remarked that not only does the underside recall in a striking manner the appearance of *Delias ornytion* and *Huphina abnormis*, but its upperside also is of a Pierine rather than of a Nymphaline character. On a superficial view there is little to distinguish it from the female of *D. ornytion* or of *H. abnormis*, and the same applies to the probably conspecific form, *M. geoffroyi*. The facies is the not unusual Pierine arrangement of a pale area surrounded by a dark border, broader in the Pierine female than in the male.

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* It is, so far as I am aware, only present among *Delias* of the *belisama* group in *D. eumolpe*, Gr. Smith, from North Borneo and *D. funerea*, Roths., from Halmaheira.

It is further remarkable that the same aspect is shared on the upperside by the male of *Nepheronia* (*Pareronia* of Bingham) *jobaea*, Boisd., the representative of its genus in Ceram, Bouru, Western New Guinea and the adjacent islands. It is well known that the females of *Nepheronia* are mimics of other butterflies, chiefly Danaines and Papilionines, that inhabit the same regions. The males, however, are not usually considered to be mimetic, with the exception perhaps of *N. tritaea*, Feld., of Celebes, *N. argolis*, Feld., of the Moluccas, and *N. phocaea*, Feld., of the Philippines. But the contrast between the uniformly-tinted ground-colour of *N. jobaea* ♂ and the black veining of the upper surface of the male *Nepheronias* from further west, such as *N. hippia*, Fabr., and *pingasa*, Moore (mainland), *naraka*, Moore (Andamans), *valeria*, Cram. (Java and Sumatra), *boebera*, Eschsch. (Philippines), is so striking as to suggest the possibility that this *Nepheronia* has been influenced in a mimetic direction by the New Guinea assemblage now under discussion. As between the *Nepheronia* and the *Mynes*, the correspondence is specially close, for it extends even to the tint of the pale area of the wing, which in neither butterfly is pure white. In both species the disc of the hind-wing is pale greyish blue; and that of the fore-wing is pale greenish yellow in the *Mynes*, and either that or very pale blue in the *Nepheronia*. It may also be remarked that the underside of *N. jobaea* ♂, by its dark hind-wing, does to some extent recall the underside of *M. doryca*, *D. ornytion* and *H. abnormis*, though it is entirely devoid of red spots or streaks. This feature of the hind-wing is exceptional in *Nepheronia*, though some approach to it is visible in *N. argolis*. A somewhat similar underside to that of *N. jobaea* ♂ is seen in *Delias ladas*, Gr. Smith, the range, however, of the latter insect appears to lie outside of the region inhabited by *N. jobaea*.

(2) It was mentioned above that *Huphina abnormis* and *H. euryxantha* are believed by some good authorities to be conspecific. Whether this be so or not, there is no doubt that the two forms are at least very closely allied. Each possesses an underside which presents a type of coloration very different from that which is usual in the genus; and it is interesting to remark that while *H. abnormis* bears a strong resemblance to one *Delias*, viz. *D. ornytion*, the very different underside of *H. euryxantha* at once recalls the *Delias* forms of the *mysis* group, particularly *D. lara*,

Boisd., which, like *euryxantha* itself, is an inhabitant of New Guinea.

It is obvious that with regard to all these forms much remains to be learned concerning their relative frequency, their exact distribution and local variation, their modes of flight and postures during rest, and the extent to which they are the prey of insectivorous birds or other enemies. Only when more data are forthcoming on these heads will it be possible to pronounce with any approach to confidence on their respective bionomic relations.

My thanks are due to Lord Rothschild, F.R.S., for personal help in examining the collections at Tring; and to Dr. Eltringham for his skilful preparations of the genitalia mentioned on p. 120.

IX. *The Geographical Factor in Mimicry.* By F. A. DIXEY, M.A., M.D., F.R.S., Subwarden of Wadham College, Oxford.

[Read March 17th, 1920.]

PLATE VI.

IN endeavouring to interpret the remarkable phenomena that are grouped under the head of Mimicry, it is important to take into account the fact that the forms resembling each other are as a general rule to be found inhabiting the same regions. This feature in the case has often received comment, and many illustrations have been adduced of the close connection between similarity of aspect and geographical proximity. The mimetic combinations of Heliconinae, Danainae, Ithomiinae and other subfamilies, modified concurrently according to their respective habitats in various parts of the South American continent and the adjacent island of Trinidad, are well known.* Other instances are certain " homoeochromatic " assemblages in the Oriental region, each comprising representatives of the Danaine, Pierine, Papilionine and occasionally the Satyrine subfamilies. These are only a few of the cases that have come to light, in which a geographical modification of a dominant form or forms has been reflected in a corresponding alteration in the aspect of the associated mimics.

The bearing of the facts here referred to on the question of the origin of mimicry is obviously of great significance; and it may be not superfluous to add a few more instances of the kind which have not hitherto met with detailed treatment or illustration. One such case is that of the parallelism between the genus *Prioneris* and certain species of the genus *Delias*, both of these genera being Pierines, though not closely related in affinity. So long ago as the year 1867 this parallelism was noted by Mr. Wallace, and subsequent investigation has tended not only to confirm, but also to extend his conclusions. Some of the mimetic pairs are figured on Plate VI; figs. 12, 14, and 16 showing the species of *Delias*, and figs. 13, 15 and 17 the forms of *Prioneris* that so closely resemble them. *D. eucharis* Drury (fig. 12), as is well known, is widely distributed in the Indian region. In Southern India and Ceylon it is joined by *P. sita* Feld. (fig. 13), which according to Fruhstorfer, flies in company with the *Delias*, and rests just like the latter with closed wings on the flowers of the Lantana. *D. belladonna* Fabr. (fig. 14) and *P. thestylis* Doubl. (fig. 15) form another geographical mimetic pair from the mountainous districts of northern India. In Borneo we have *D. indistincta* Fruhst. (fig. 16) and its very exact copy *P. cornelia* Vollenh. (fig. 17). Other mimetic pairs not here figured are *D. egialea* Cram. with *P. hypsipyle* Weym. of Sumatra, and *D. crithoe* Boisd. with *P. autothisbe* Hübn. of Java. The two latter species are said by Fruhstorfer to visit the flowers of cinchona in each other's company.

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* See Poulton, " Essays on Evolution," 1908, pp. 272, 273.

A remarkably interesting mimetic series is shown in figs. 4 to 11 of Plate VI. Fig. 5 represents the underside of *H. laeta* Hew. of Timor, a butterfly whose aspect differs so greatly from that of its congeners as to have suggested to Mr. Wallace the possible existence of a model belonging to the *belisama* group of *Delias*. Thirty-four years after the date of Wallace's paper, the missing model turned up in the person of a fine *Delias* discovered in Timor by Mr. Doherty, and named *D. splendida* by Lord Rothschild (fig. 4). Though the resemblance between the *Delias* and the *Huphina* is deceptively close, there is yet a difference to be observed in the fact that *H. laeta* possesses a row of marginal scarlet spots on the hind-wing which are not to be found in *D. splendida*. But before leaving Timor Mr. Doherty completed the assemblage by finding another *Delias*, named *D. dohertyi*, after its discoverer, by Lord Rothschild (fig. 6). In this butterfly the resemblance to the two former species is close; and it possesses, which *D. splendida* does not, a row of scarlet spots running parallel with the outer border of the hind-wing. On the other hand, the scarlet costal streak, conspicuous in *D. splendida* and *H. laeta*, is absent from *D. dohertyi*. The *Huphina* therefore may be said to combine in itself two characteristic features which are found separately in the two *Delias* models.

We may now turn to the islands of Lombok, Sumbawa and Flores, where we find geographical representatives of all three members of the Timor assemblage. It is interesting to observe that just as the members of the South American mimetic associations undergo a simultaneous change corresponding to a different locality, so does the *Delias–Huphina* combination in all three of its members alike.

The *Huphina* in the islands of Lombok, Sumbawa and Flores which represents *H. laeta* of Timor is *H. temena* Hew. (fig. 8). The *Delias* corresponding to *D. splendida* is *D. oraia* (fig. 7), and the *Delias* answering to *D. dohertyi* is *D. sumbawana* (fig. 9). In all three of the Lombok, Sumbawa and Flores assemblage, the uniformly black fore-wing of the Timor butterflies is replaced by a pale ground-colour streaked with black (the black streaks being nervular in the *Huphina* and internervular in the two *Delias*); the scarlet costal streak is also less definitely black-bordered in *H. temena* and *D. oraia* than in *H. laeta* and *D. splendida*; while the marginal scarlet spots have a more strongly-marked dark bordering in *H. temena* and *D. sumbawana* than in *H. laeta* and *D. dohertyi*, their counterparts in Timor.

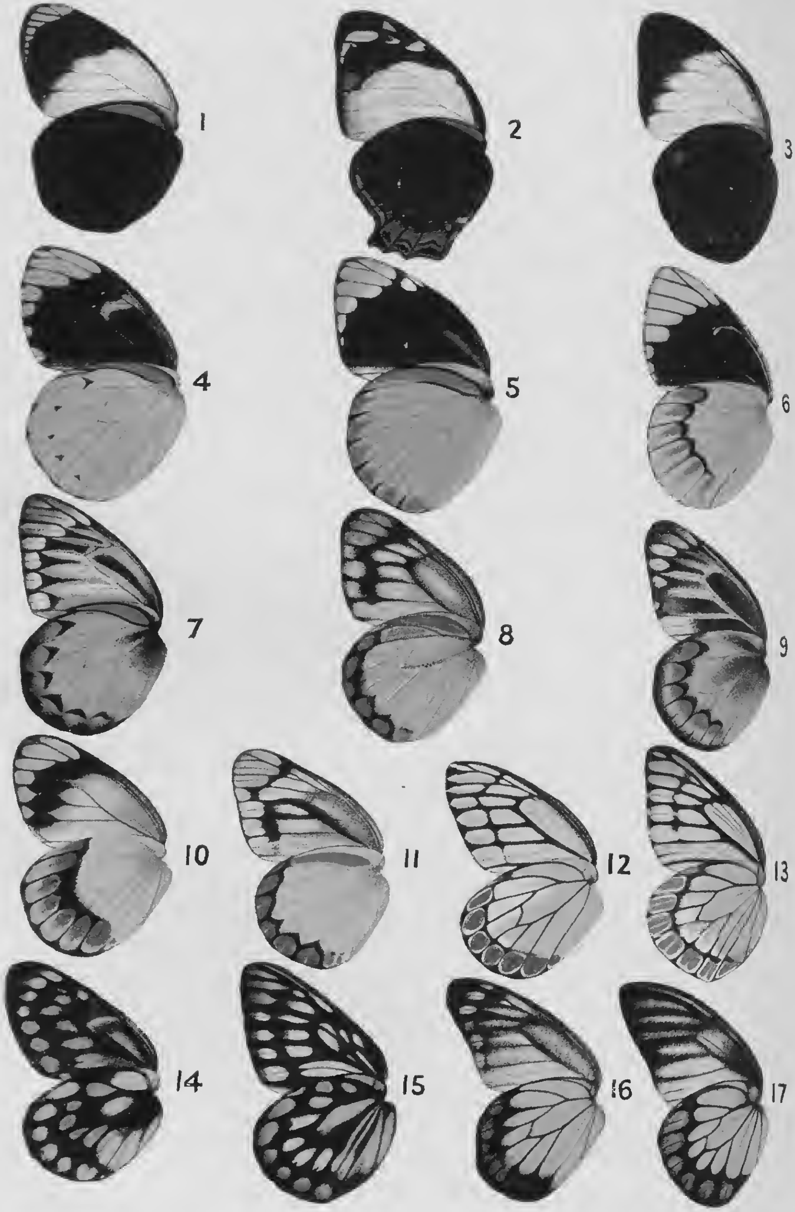
Finally, in the island of Sumba occurs another representative of *H. laeta*; viz., *H. julia* Dohert. (fig. 11), another of Doherty's discoveries. Along with it is found a *Delias*, *D. fasciata* Roths. (fig. 10), which bears the same relation to *H. julia* as *D. sumbawana* to *H. temena*. A *Delias* corresponding to *D. splendida* and *D. oraia* has, so far as I am aware, not yet turned up in Sumba, but it may be not too rash to anticipate that a model may some day be found to account for the scarlet costal streak in *H. julia*, which is absent from its associated *Delias*.

Attention may likewise be drawn to the three New Guinea butterflies whose undersides are represented in Plate VI, figs. 1, 2 and 3. Here again we have an association between a *Delias* (*D. ornytion* Godm. and Salv., fig. 1) and a *Huphina* (*H. abnormis* Wallce., fig. 3). In this case the company is joined by a Nymphaline, *Mynes doryca* Butl. (fig. 2). As I have dealt somewhat fully with these butterflies in a recent paper (Trans. Ent. Soc. Lond., 1918, pp. 118–129), I need say no more about them on the present occasion, except to notice the fact, previously alluded to, that in the ordinary position of rest, with the fore-wings depressed, the scarlet streak on the hind-wing of the *Mynes* will be found to correspond more or less exactly with the similarly coloured streak on the fore-wing of the *Huphina*, and the scarlet patch on the hind-wing of the *Huphina* with a similar patch on the fore-wing of the *Mynes*. This, like the position, with regard to the veins, of the streaks on the fore-wing of the Lombok butterflies, provides a further illustration of a principle frequently to be observed in mimicry; viz. that the mimetic assimilation aims only at the general effect of the resemblance, and is apt to ignore considerations of mere homology.

As to the cause and mode of origin of these startling likenesses, every one must interpret the facts as he sees fit. It is doubtless the case that more data are wanted before the question can reach a final settlement. I would only plead that in all attempts at a solution, account must be taken of the geographical factors. And it does not seem to me possible to bring instances like the present under such headings as that of the common colouring shared by the inhabitants of desert areas or of the arctic snow-fields. Nor is it easy to imagine any external conditions of soil or climate which could directly bring about a common scheme of colouring like that of the three New Guinea butterflies, or of the pairs and triads from India and the Malay islands respectively which are shown on Plate VI. For my own part I confess that I am still of opinion that adaptation is at the bottom of the matter; and in spite of much adverse criticism I find it hard to resist the conviction that in the theory of warning colours shared between comparatively distasteful, or deceptively adopted by comparatively palatable forms, we have by far the most probable explanation as yet advanced.

EXPLANATION OF PLATE VI.

[*See Explanation facing the* PLATE.]



MIMICRY IN EASTERN BUTTERFLIES.

EXPLANATION OF PLATE VI.

Fig.			
1.	Delias ornytion	*Godm. & Salv.*	New Guinea
2.	Mynes doryca	*Butl.*	,,
3.	Huphina abnormis	*Wallce.*	,,
4.	Delias splendida	*Roths.*	Timor
5.	Huphina laeta	*Hew.*	,,
6.	Delias dohertyi	*Roths.*	,,
7.	Delias oraia	*Dohrt.*	Lombok, Sumbawa, Flores
8.	Huphina temena	*Hew.*	,,
9.	Delias sumbawana	*Roths.*	,,
10.	Delias fasciata	*Roths.*	Sumba
11.	Huphina julia	*Dohrt.*	,,
12.	Delias eucharis	*Drury*	India, Ceylon
13.	Prioneris sita	*Feld.*	S. India, Ceylon
14.	Delias belladonna	*Fabr.*	N. India
15.	Prioneris thestylis	*Doubl.*	,,
16.	Delias indistincta	*Fruhst.*	Borneo
17.	Prioneris cornelia	*Vollenh.*	,,

IV. *On Specific and Mimetic Relationships in the genus* Heliconius, *L.* By H. ELTRINGHAM, M.A., D.Sc., F.Z.S.

[Read March 1st, 1916.]

PLATES XI–XVII.

SOME time has elapsed since Professor Poulton first suggested to me that an investigation into the specific relationships of the forms of the genus *Heliconius* would probably be productive of interesting results, and I must admit to having had some hesitation in embarking on such a work in view of the fact that a very lengthy and elaborate monograph of the genus already existed. This memoir, however, is based entirely on external characters, and it appeared that anatomical study might elucidate new facts with regard to the relationships of the forms, more especially as the mimetic phenomena are of an unusually complicated kind.

Perhaps the most valuable feature of the monograph above referred to (Stichel and Riffarth, in "das Tierreich," 1905) is the recognition by Riffarth that the whole genus can be divided into two sections by means of a peculiar character of the fore-wing underside in the male. It was my friend, Mr. W. J. Kaye, who pointed out * that, having divided the forms by means of the character mentioned, a most remarkable fact was disclosed.

A great number belonging to Section I resemble very closely forms belonging to Section II. In other words, intrageneric mimetic resemblance is of frequent occurrence. I here use the words "mimetic" resemblance in a wide sense as indicating merely a similarity of pattern; the precise nature of the resemblance may be considered later.

The present paper is an attempt to investigate more precisely the specific relationships of the forms of *Heliconius* by means of anatomical study combined with an examination of pattern gradations.

We are rarely able in such investigations to arrive at entirely satisfactory conclusions owing to lack of adequate material and data, and I fear the present effort is no exception. The results may, however, serve to indicate the directions in which future workers, and especially those with facilities for making breeding experiments, may hope to obtain more definite results. For the opportunity of examining and dissecting many rare forms I am indebted to the generosity of Lord Rothschild, Mr. W. J. Kaye, and the Authorities of the British Museum, whilst my friend Professor Poulton has assisted me with his continual encouragement and valuable suggestions. Mr. Kaye has also given me much practical help in sorting specimens and in correspondence, and my friend Dr. F. A. Dixey has rendered valuable assistance in connection with Pierine mimics. Dr. Karl Jordan has kindly looked over most of my microscope preparations and given me the benefit of his views thereon.

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* Proc. Ent. Soc. Lond., p. xiv, 1907.

Opinions may differ as to the significance of conclusions based on the structure of the male armature. However that may be, probably most naturalists will agree that close resemblance in these structures may usually be regarded as evidence of near relationship, whilst distinct and constant differences will probably generally be accepted as evidence of specific separability.

In the genus *Acraea* it was found that in nearly all cases the species were well defined, and anatomical differences easily recognised. Such is only partially the case in *Heliconius*, as will be seen later, nor are the structures particularly constant within the limits of the same species. It should be understood at the outset that I do not put forward the present paper as a statement of conclusive and final results, hence it is not to be taken as a complete revision of the genus. I do not consider that our knowledge of the forms is yet adequate to such a task. My desire has rather been to indicate the directions in which future effort should be made, and the lines on which, especially, those in the field might profitably direct their observations.

The genus is distinguished from *Eueides* by its much longer antennae. It can be divided, as Riffarth has shown, into two great sections. On the underside of the male fore-wing, from the inner margin to the first branch of the median, is an area which presents a peculiar silky grey appearance. In Section I of the genus this silky surface is continued right up to the median without any visible change in texture. In Section II there is, adjacent to the median and its branch, a certain amount of dull "mealiness." This amount may be very small, but it is always recognisable, especially after a very little practice. The two sections were designated by the extremely clumsy names of Opisogymni and Opisorhypari respectively. For convenience they may be referred to as Section I and Section II. Between these two sections the reputed species are nearly equally divided. In the monograph referred to Section I contains 31 species and 110 subspecies, whilst Section II includes 39 species and 79 subspecies. This division is apparently a natural one, and so far as my preparations go the genital armature of no species of Section I could be mistaken for that of a species of Section II.

Section I may now be further divided, and we will first consider the forms included by Riffarth under the name Silvaniformes. These include nearly all those species the patterns of which are composed of yellow, brown, white, and black markings. Generally speaking, it may be said that the ground-colour of one or both wings is brown or yellow, though there are one or two exceptions.

The evidence of the genitalia.

Whilst the genitalia of nearly all the members of this group are readily distinguishable from those of the rest of the genus, they are by no means so readily separable *inter se*. Moreover, at least one form hitherto regarded as rather widely separated from the Silvaniformes must now be included in that group. I refer to *H. atthis*. In the accompanying plates the genitalia have been illustrated by giving a carefully drawn outline of one clasper, as it is from the shape of this part that any conclusions can best be drawn.* After examination of a large number of preparations, it appears that they may be divided more or less into those which have a dense hairy tuft near the end of the clasper and those which are only moderately pilose. Whether this feature is of real value or not is difficult to decide; if, however, we accept the feature it would seem possible to separate the following reputed species and their forms from the remainder of the Silvaniformes.

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* I much regret the poor quality of these plates. The present necessity for economy has, however, made it impossible to use the beautiful lithographic process by which the figures were reproduced in my paper on *Acraea*.

H. ismenius.
,, *"silvana" metaphorus.*
,, *narcaea.*
,, *numatus.*
,, *ethilla.*
,, *gradatus.*

The first two above are separable from the rest on general differences in the armature, and we may now consider the remainder.

H. narcaea, Godt.

The typical form of this well-known species occurs in S. Brazil. In Seitz' ab. *connexa* the subapical band is completely separated and surrounded by black. The form *satis*, Weym., has a brown instead of a yellow band in the hind-wing. The form *flavomaculatus*, Weym., has a yellow instead of a white apical spot in the fore-wing, whilst *physcoa*, Seitz, has the fore-wing yellow band much broader than usual. The form *polychrous*, with largely increased black areas, is regarded by Stichel and Riffarth as a subspecies, though apparently occurring in the same localities as *satis*. It cannot be doubted that these are all forms of the same species, as they are for the most part mere colour variations. The outline of the claspers in three of the forms is shown on Pl. XIII. In general structure there is considerable agreement, though there is a marked difference between the actual outlines of the typical form and *narcaea polychrous*.

H. numatus, Cram.

Of this species some ten forms have been named, and they extend from Guiana across North Brazil to the Western Amazon region and Peru. The claspers of three forms are illustrated on Pl. XIII. The form *guiensis* is merely a variety of the type, but there is a greater difference between its clasper and that of *numatus numatus* than between the latter and *narcaea narcaea*. Indeed, the two last are not appreciably distinguishable. It may be said that they do not occur in the same locality and that thus there is no necessity for the respective armatures to be different.

There may be something to be said for this view, though it will not explain further cases yet to be described.

H. silvana, Cram.

Of this form three subspecies are named, and though the genitalia of the group are of little assistance in many of the cases of closer resemblance they seem to show that at least three of the forms hitherto regarded as subspecies of *silvana* do not belong to *silvana* at all, but to two other species. On Pl. XIII I have shown the claspers of two specimens of *silvana silvana* taken at random. One is hardly distinguishable from *numatus guiensis*, whilst the other is but little modified from *narcaea narcaea*. A part of the difference is due to the bending over of the apex of the clasper, but this is not a point of great importance and probably would not occur in a perfectly fresh specimen. Now, *silvana* occurs in Guiana, Venezuela, N. Brazil and Peru. The anatomy of the armature gives no reason to suppose that it is anything but a form of *numatus*, just as the latter on the same grounds appears to be as closely related to *narcaea*.

H. ethilla, Godt.

Some twelve forms of this species have been named, ranging through Trinidad, Guiana, Brazil, Venezuela, Colombia, and Panama. Seven illustrations of the claspers are given on Pl. XIII. The two specimens of *ethilla ethilla* are by no means identical, whilst the two of *ethilla tyndarus* are markedly different. One example of *ethilla ethilla* resembles *narcaea satis* and is not unlike *numatus numatus*. The outline of *ethilla aërotome* is very different from one example of *ethilla ethilla*, but not sufficiently distinct from one of *ethilla tyndarus*. My friend Mr. W. J. Kaye, regards *ethilla* as conspecific with *numatus*, a view I am strongly inclined to support, further adding that so far as the armatures are concerned there is no more reason for separating either from *narcaea* and *silvana*.

H. gradatus, Weym.

Of this rather rare species I have been able to make only one preparation from its subspecies, *thielei*, Riff. As will be seen from the illustration on Pl. XIII, the clasper is much less different from that of *ethilla metalilis* than the latter is from some other forms of *ethilla*.

We thus see that on the structure of the genitalia we cannot satisfactorily distinguish between *narcaea*, *numatus*, *ethilla*, and *gradatus* and most of their forms.

We now turn to a large group containing ten reputed species and their forms. They all have at least this feature in common, that there occurs near the end of the clasper a tuft of bristles sufficiently evident to distinguish them from those of the *narcaea* group.

H. novatus, Bates.

The claspers of the three principal forms are shown on Pls. XIII, XIV, and present a closer agreement than any we have so far examined. The forms are found in Peru and Bolivia. Mr. Kaye informs me that *schultzei*, Riff., is merely the female of *novatus*.

H. hecale, Fab.

This large black form with a conspicuous white patch on the fore-wing occurs in Dutch and British Guiana. The clasper is shown on Pl. XIV, and differs in scarcely any respect but that of size from those of the last and next species. There is a form named *fulvescens*, Lathy, from Demerara, in which there is a brown basal suffusion in the fore-wing.

H. aristiona, Hew.

Of this species some twelve subspecies and several forms have been named, ranging through the Amazon region, Peru, Ecuador and Bolivia. I have shown the claspers of seven forms on Pl. XIV, and here again there is considerable general agreement accompanied by a certain variation in actual outline.

H. ithaka, Feld.

The typical form and two subspecies are all found in Colombia. It would be difficult to distinguish between the clasper shown on Pl. XIV and that of some of the forms of *aristiona*.

H. pardalinus, Bates.

The type form and four subspecies range through N. Brazil, Peru, Bolivia and probably Ecuador. The clasper of *pardalinus lucescens* shown on Pl. XIV is shorter and broader than those already considered, yet, except in size, there is no very satisfactory difference between it and that of *anderida zuleika* on Pl. XV, and some forms of *anderida* are barely separable from *aristiona*.

H. fortunatus, Weym.

This and two subspecies occur in N. Brazil. I have illustrated a clasper of *fortunatus spurius* on Pl. XIV. It is much more rounded than those so far considered. If every specimen dissected out were identical with this, then we might, perhaps, say that it differed constantly from the other species, but a very small amount of variation would make it as difficult to distinguish as the rest.

H. quitalenus, Hew.

The type form and three subspecies range through Peru, Ecuador, Bolivia and N. Brazil. Reference to the drawings on Pl. XIV shows a marked difference between *quitalenus quitalenus* and *quitalenus felix*. The first might well be a variation of one of the forms of *novatus*. If the second differs from these it does so no more than from its own type.

H. anderida, Hew.

The type and six subspecies range through Venezuela, Colombia, Central America, and one form is said to have been taken in Dutch Guiana. The claspers of six forms are illustrated on Pls. XIV, XV, from which it may be seen that there is considerable variation. There is less difference between *anderida holocophora* and *aristiona floridus* than between the former and *anderida anderida*. Kaye is of opinion that *anderida fornarina* is either a good species or a form of *hecale*. The clasper is, however, very near to that of *anderida melicerta*, and though *hecale* has a somewhat different appearance it still seems connected with the other forms of this group.

H. paraënsis, Riff.

The two forms of this species are described from Para and Itaituba respectively. A clasper of the form *latus*, Riff., is illustrated on Pl. XIV, and is seen to be not satisfactorily distinguishable from several of the other forms described.

H. aulicus, Weym.

I have only had one example of this species to examine. Its clasper is shown on Pl. XV. It has the dense hairy tuft of the *novatus* group, and differs little from that of *aristiona tarapotensis.* The pattern of the wings is also so similar that it seems certain that they are the same species.

All the above seem to constitute a group of forms which cannot be constantly distinguished by the genitalia. Before passing to those species which have claspers of the *ismenius* type there are a few forms which must be separately considered.

H. "silvana" robigus, Weym.; **H. "silvana" ethra,** Hübn.

The form *robigus* occurs in Brazil (Espiritu Santo, Rio de Janeiro, Minas Geraes, etc.). The clasper is shown on Pl. XV. It cannot be placed in the *narcaea* group owing to its form. It is less densely tufted than those of the *novatus* group. Two preparations show much the same structure. It is certainly incorrectly placed in being associated with *silvana.* Apart from the difference in the tuft, the form of the clasper suggests an affinity with *aristiona,* and further reasons for placing it in that association will be given later.

The clasper of "*silvana*" *ethra* shown on Pl. XV is barely distinguishable from that of "*silvana*" *robigus.* It is rather more densely tufted, but must, I think, be regarded as conspecific with *robigus* and probably with *aristiona* and *novatus.*

H. vetustus, Butl.

The typical form occurs in British Guiana and the form *metellus,* Weym., in N. Brazil. The clasper (Pl. XV) is of a curiously irregular shape. Except for the dense tuft of bristles it might well be a form of *numatus.*

H. sergestus, Weym.

This species occurs at Tarapoto in Peru. I have had but one example to examine, and the clasper is shown on Pl. XV. If its well-rounded and tufted form is constant it may well be regarded as definitely distinct.

H. atthis, Doubl.

This species, which has become so profoundly modified in mimicry of *Tithorea pavonii,* occurs in Ecuador. Though hitherto regarded as related to the Cydnoformes, the structure of the clasper on Pl. XV shows it to belong rather to the Silvaniformes. If it had a denser tuft of bristles it would be difficult to distinguish it from *aristiona lenaeus.*

H. ismenius, Latr.

The typical and four subspecies occur in Colombia and Central America. Though the forms are placed near *narcaea* in existing works, I have placed them nearer to the latter part of Section I, since, if the form of the claspers is to be regarded as any indication of relationship, then they are undoubtedly closely allied to the *melpomene* association. The claspers of three forms are shown on Pl. XV, from which it will be noted that there is some variation between them. The clasper of "*silvana*" *metaphorus* is also shown, and is seen to resemble that of *ismenius telchinia* so closely that we cannot doubt that the form is much more closely related to *ismenius* than to *silvana.* Indeed, I am convinced that it is merely another form of *ismenius.*

We have now considered nearly all the reputed species which appear to belong to the group Silvaniformes. Forms of which I have been unable to obtain examples are *ennius*, *sulphureus*, and *hippola.* With so peculiar a genus it may be rash to speculate on the position of forms which have not been examined, but I should expect *ennius* to prove a form of *quitalenus*, and *sulphureus* of *ethilla.* As to the rare species, *hippola*, of which only the type seems to be known, its appearance gives no clue. It will, perhaps, prove to be near *narcaea.*

Assuming the structure of the genitalia to be of any value at all in these forms, we can, therefore, arrange the reputed species in six groups of which it may be said that if the respective members are not conspecific, at least they are extremely closely allied, and are not separable by any constant and recognisable features of the male armature.

I have left for consideration at the end of this group two species which are amongst the most remarkable of all the Heliconii. The first is *H. tumatumari*, Kaye, from Guiana. This species resembles *aoede astydamia*, forms of *erato*, and secondarily forms of *melpomene.* It is a tribute to Mr. Kaye's excellent judgment that he did not regard it as a form of *melpomene*, but described it as a separate species. The structure of the male armature is quite different from that of any form of *melpomene*, and, in fact, has a typically silvaniform appearance. It is nearest to that of a species with which one would not at first think of associating it, viz. *vetustus*: indeed, the only obvious difference between the armature is that in *vetustus* the extremity of the clasper is rather more densely pilose. That the species is, in fact, closely related to *vetustus* I have no doubt, and the further evidence for this will be found under the discussion of patterns. It may here be mentioned that the most obvious difference between *tumatumari* and *melpomene* forms is the occurrence in the former of a sulphur yellow streak on the underside of the hind-wing, this streak being not *on* the costa, but below the costal nervure.

On my pointing out to Mr. Kaye the significance of this yellow line, he kindly brought for examination two *melpomene*-like forms, one of which agrees with *melpomene elevatus*, Nöld., and the other an undescribed female form somewhat like it, from his own collection. Both these had the peculiar yellow line, and without anatomical examination might well have been regarded as geographical forms of *tumatumari*. Microscopic investigation of the male example showed, however, that though it was apparently not a form of *melpomene*, it was equally specifically separate from *tumatumari*. The armature is again of a somewhat silvaniform type, but resembling that of *H. sergestus*. These two species, *elevatus* and *tumatumari*, will be further considered in the discussion of patterns.

Although they are separable from *melpomene* it must not be supposed that they are as markedly distinct from that species as are many of the species of Section II from one another. Preparations of the genitalia of *melpomene* show much individual variation, and whilst there would never be any difficulty in distinguishing the armatures of, say, *anderida* and *melpomene*, there might be more difficulty in separating some preparations of *melpomene* from certain of the Silvaniformes. In other words, the Silvaniformes are not, in spite of their *Melinaea*-like patterns, a markedly separate group, and, in fact, it may be said that all the species belonging to Section I are far less satisfactorily differentiated than those of Section II. This fact would seem to lend support to the view that Section I is of more recent development, as we should expect, since its members are mimics rather than models.

We now pass to those species grouped under the name of the

CYDNOFORMES.

H. cydno, Doubl.

The typical and eight subspecies are described with several varietal forms occurring in Central America, Peru, Ecuador, Colombia, and Venezuela. The claspers of five forms are shown on Pl. XV. They show a general resemblance of structure with a certain amount of variation.

H. weymeri, Stgr.

Of the typical form of this Colombian species I have had no example to examine, but have dissected out more than one armature from the form *gustavi*, Staud. There is no constant and recognisable difference between the armatures of this and of *cydno* (Pl. XV).

H. pachinus, Salv.

This species from Chiriqui and Costa Rica occurs commonly in collections. I have made several preparations which show but little range of individual variation. The pattern of the wings seems at first sight so distinct that it might well be regarded as a satisfactorily defined species, yet the armature (Pl. XVI) shows no distinction from that of *weymeri* and could not be constantly separated from some forms of *cydno*.

H. heurippa, Hew.

This species, with which I include *rubellius* of Smith and Kirby, occurs in Colombia. Typical *heurippa* has a striking appearance owing to the large patch of sharply divided yellow and red on the fore-wing. In the form *rubellius* this patch is reduced to very narrow dimensions. The clasper shown on Pl. XVI from a specimen of *heurippa* shows much the same structure as is found in *cydno*, *weymeri*, etc. There can be little doubt that *heurippa* and *cydno* are the same species, and it will be seen later that consideration of the pattern confirms this view.

H. melpomene, Linn.

Over fifteen subspecies of this form, with many varieties, are described. They range over the greater part of northern S. America, but have not, so far, been reported from Colombia and Venezuela. A drawer filled with these forms presents a most bewildering diversity of patterns linked together by intermediate forms. On Pl. XVI I have illustrated eight of the claspers. From these it will be seen that there is a strong tendency for the point of the clasper to be fuller and more rounded than in *cydno* and some of the other forms. Two drawings are shown taken from consecutive specimens of *melpomene thelxiope*. The difference between these is as great as that between the second of them and one of the *cydno* forms, whilst that of *melpomene timareta contiguus* is essentially of the *cydno* pattern.

H. amaryllis, Feld.

The typical and two subspecies occur in Central America, N.W. Brazil, Peru, Venezuela, Colombia and Trinidad. Of the two claspers shown on Pl. XVI that of *amaryllis rosina euryas* is of the *cydno* type, whilst that of *amaryllis euryades* comes nearer to that of some forms of *melpomene*, showing that here again this reputed species cannot be definitely separated.

H. vulcanus, Butl.

The typical form occurs in Colombia and Panama, and is rather doubtfully recorded from Guiana. The form *cythaera*, Hew., occurs in Ecuador. Claspers of the two forms are shown on Pl. XVI, and present no clearly distinguishing features.

H. xenoclea, Hew.

This species appears as *batesi* in Stichel and Riffarth's monograph, Riffarth having thought that *xenoclea* belonged to the second section of the genus. Kaye pointed out the error,* and has given the name *microclea* to the form in Section II which resembles Hewitson's species. It occurs in Ecuador and Peru, and is distinguished by the two separate rounded spots on the fore-wing.

The clasper figured on Pl. XVI is not distinguishable from several of those already described.

H. nanna, Stich.

This reputed species occurs in S. Brazil, and a form occurring further north, in which the fore-wing red discal band is less indented, has been named *burchelli* by Poulton. *H. nanna* resembles closely, on the upperside at least, *H. besckei*. The clasper as shown on Pl. XVI is no more distinctive than the others already considered.

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* Proc. Ent. Soc. Lond., p. xiv, 1907.

H. besckei, Ménétr.

This species, occurring in S. Brazil, resembles *nanna* and *erato phyllis*. It is distinguished outwardly by a reddish submarginal line on the underside of the hind-wing. Kaye has expressed the view that it is a form of *H. erato phyllis*, but the structure of the armature precludes this possibility. A clasper is shown on Pl. XVI, and the principal feature in which it differs from the *cydno* and *melpomene* forms is the presence of a dense tuft of bristles near the point. If this be a good character, as has been supposed, in dividing the Silvaniformes, then we have grounds for separating the species, and the peculiarity of the hind-wing pattern supports this view.

We thus see that in so far as may be judged from the genitalia there is no reason to suppose that the forms now included under the Cydnoformes and Melpomeneformes, with the exception of *H. besckei*, really constitute more than one species. The extent to which pattern and other features support such a conclusion will be discussed in a later portion of this paper.

SECTION II.

In this section the structure of the armature provides much more satisfactory evidence of specific distinctions and to a considerable extent confirms the reputed species into which the forms have been divided. Taking these in the order adopted in Stichel and Riffarth's work, we find seven reputed species included in group I, the

HECALESIFORMES.

H. crispus, Stgr.

This species resembles *atthis*, but is modified so as to mimic *Tithorea bonplandii descandollesi*. It occurs in the Cauca valley. I have had no specimen to examine.

H. hecuba, Hew.

This Colombian species also resembles a *Tithorea*. Seitz regards both *choarinus* and *cassandra* as forms of this species, together with *tolima*, Fassl. I have had *hecuba*, *choarinus* and *tolima* to dissect, and they would certainly appear to be the same species. The claspers of *hecuba* and *choarinus* are shown on Pl. XVI. That of *cassandra* I have not been able to examine.

H. hecalesia, Hew.

The typical form occurs in Colombia and the form *formosus* in Guatemala, Nicaragua, Costa Rica, and Panama. I have dissected examples of both, and the clasper is shown on Pl. XVI. It is of quite distinct structure. *H. octavia*, Bates, has exactly the same type of clasper and is certainly the same species. It occurs in Guatemala and Honduras.

Two forms of this group remain, *H. gynaesius*, Hew., and *H. longarenus*, Hew. The first of these Riffarth regards as a form of *hecalesia*. Unfortunately, I have had no example to examine, and the only specimen of *longarenus* known to me is the type. My view as to the position of these two forms will be found under the consideration of patterns.

AOEDIFORMES.

H. godmani, Stgr.

This species is included by Riffarth in the Aoediformes, but its appearance suggests an alliance with *gynaesius*, though this may quite well be due to mimetic resemblance. I cannot express an opinion as to its true position, as the type is, so far as I know, the only specimen in existence. It was taken on the river San Juan in W. Colombia.

H. metharme, Erich.

A rather distinctive-looking species occurring in N. Brazil, Peru, Colombia, and doubtfully in Nicaragua. The male armature (Pl. XVI) is quite distinct from that of any other form examined except *aoede*.

H. aoëde, Hübn.

The typical and three subspecies range through British Guiana, N. Brazil, Venezuela, Peru, and Ecuador. The claspers of two forms are illustrated on Pl. XVI. They differ from one another considerably, but the differences are just such as to make it difficult to separate them on these structures from *metharme*. In the latter species the peculiar toothed organ on the inner side of the clasper seems intermediate in form between that of *aoede aoede* and that of *aoede astydamia*. Allowance must be made for differences of position, as this organ appears to be movable. The matter will be further considered under the discussion of patterns.

XANTHOCLEDOFORMES.

H. xanthocles, Bates.

Five subspecies and the typical form are described from various parts of northern S. America. The male claspers are distinctive, those of two forms being shown on Pl. XVI. The most interesting feature is the small, upturned projection from the inside of the clasper, suggesting an alliance with *H. hierax*, Hew.* The only feature of the wing patterns which would support such a view is the row of small, almost marginal white spots on the underside of the hind-wing.

EGERIFORMES.

H. egeria, Hübn.

The typical and three subspecies of this large and handsome form have been described from Guiana and North Brazil. The male clasper is illustrated on Pl. XVI, and could not be confused with that of any other species I have examined, though suggestive of relationship with *burneyi catharinae*.

H. burneyi, Hübn.

The typical form and three subspecies range through Guiana, N. Brazil, Peru, Bolivia, and Colombia. I have illustrated the claspers of three forms (Pl. XVII) showing a very wide limit of variation, notwithstanding which, the clasper of only one other reputed species could be confused with them. This is *wallacei wallacei*, Pl. XVII, and it is difficult to see in the armature any grounds for regarding it as specifically distinct. *H. wallacei colon* shows a similar structure.

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* On the clasper alone *hecuba*, *xanthocles*, and *hierax* would appear to be rather difficult to separate. There are certain other differences, however, notably in the shape of the uncus, which enable them to be separated.

H. doris, Linn.

The forms of this species have a wide range, being recorded from the whole of northern S. America. It is characterised by the radiate coloured markings on the hind-wing, which may be blue, green, or red, or combinations of these, or even dusted with white. Three subspecies and some varietal forms are described. I have illustrated on Pl. XVII the claspers of only two forms, as further preparations show a similar structure characterised by a large upturned projection of the upper part of the clasper. No other species can be confused with it.

H. hierax, Hew.

I have already pointed out that the clasper of this species suggests a close affinity with *H. xanthocles*. It is certainly wrongly placed next to *doris*.

WALLACEIFORMES.

H. wallacei, Reak.

The typical and two subspecies are described from northern S. America. As indicated above, the claspers (Pl. XVII) show a near affinity, if not specific identity, with *burneyi*.

SAPHOFORMES.

H. sapho, Drury.

The typical and four subspecies are described from Peru, Ecuador, Colombia, Central America, and doubtfully from Jamaica. The claspers of two forms are shown on Pl. XVII, and those of other forms examined show a similar structure. They suggest relationship with the Clysonimoformes, though they are distinguishable from the fact that in the latter the lower inflated part of the clasper is of a thinner chitin. There seems little to separate the *sapho* forms from *antiochus*, *leucadia* and *sara*.

H. hewitsoni, Stgr.

This species is remarkable for its resemblance to *H. pachinus*. Though allied to *sapho* forms I think it is certainly distinct, the male armature having several peculiarities (Pl. XVII).

H. congener, Weym.

This species is closely allied to the *sapho* forms, but the uncus is much more slender, so that for the present we may keep it separate (Pl. XVII).

ANTIOCHIFORMES.

H. antiochus, Linn.

This species and four subspecies are described from Guiana, Brazil, Peru, Ecuador, Colombia, and Venezuela. A remarkable form, *salvinii*, Dew., from the Orinoco delta, has a transverse yellow hind-wing band (Pl. XVII).

H. leucadia, Bates.

The type and one subspecies are described from N. Brazil, Peru, Ecuador and Bolivia (Pl. XVII).

H. sara, Fab.

Six subspecies of this form are described from various localities ranging through the greater part of northern S. America. Claspers from the above three reputed species are illustrated on Pl. XVII, from which it will be seen that, though varying in size and slightly in form, there is no satisfactory feature to distinguish them either from each other or from *sapho* forms. Also, it may be observed, they approach in structure the *cydno* forms.

ERATOFORMES.

H. himera, Hew.

A small and interesting form from Ecuador.

H. notabilis microclea, Kaye.

Resembles *H. xenoclea*, Hew., but distinguished by the character of the section. Occurs in Peru and Ecuador. A form with the fore-wing spots more or less white occurs in E. Ecuador.

H. cyrbia, Godt.

The typical and two subspecies are described from Ecuador, Colombia, and Bolivia.

H. favorinus, Hopff.

A Peruvian form.

H. petiveranus, Doubl.

The typical and one subspecies described from Colombia, Venezuela, and Central America.

H. hydarus, Hew.

Five subspecies are described. The forms occur in Venezuela, Trinidad, Colombia, and Panama. The forms are remarkable for the great diversity of colour and pattern exhibited.

H. amphitrite, Riff.

A Peruvian species closely resembling *erato callycopsis viculata.*

H. erato, Linn.

The typical and no less than eleven subspecies are described. Extending over the greater part of northern S. America. It is a species in which pattern and colour seem to run riot much as in *melpomene.*

Claspers taken from the foregoing eight reputed species are illustrated on Pl. XVII. All are characterised by the toothed projection at the outer end of the clasper, which takes the form of a flattened lobe with a peculiar twist, as though it had been taken in forceps and given part of a turn, whilst the rest of the clasper remained fixed. An examination of the figures shows that no satisfactory character differentiates these forms. The figures are only a selection from many preparations, all of which show the same kind of structure. Whether or not all are forms of one species, they certainly cannot constantly be distinguished by the structure of the armature.

One more species of the group remains, viz.—

H. hermathena, Hew.

This remarkable species from the Lower Amazon region has the fore-wings of one of the *erato* forms and the hind-wings of *H. charithonia*. The clasper shows a near relation to *erato*, but there is a peculiar formation below the twisted projection, giving it the appearance of having been pinched (Pl. XVII).

CHARITHONIFORMES.

H. charithonia, Linn.

A common and well-known species having a very wide range over S. America and even into southern N. America. The clasper is very small for the size of the insect, and though not very characteristic may probably be regarded as distinct (Pl. XVII). There is one subspecies, *peruviana*, Feld., in which the claspers are similar.

H. nattereri, Feld.

Of this rare Brazilian (Bahia) species I have had no example to examine.

H. fruhstorferi, Riff.

Resembles the above and is thought to be its female. I have not seen an example.

CLYSONIMOFORMES.

H. clysonimus, Latr.

The typical and two subspecies are described from Central America, Colombia, and Venezuela. The principal characteristic feature of the clasper, shown on Pl. XVII, is the compressed appearance of the end of the dilated portion.

H. hortense, Guér.

From Ecuador, Colombia, Guatemala, and Honduras. The clasper (Pl. XVII) has a curious little hook-like projection.

H. telesiphe, Doubl.

From Peru and Bolivia. A form with yellow instead of white band on hind-wing (*sotericus*, Salv.) occurs in Ecuador. The clasper on Pl. XVII is simple and not very characteristic. Though somewhat resembling *sapho* forms, the uncus (not shown) is of a stouter form and slightly toothed.

We have now considered the apparent relationships of most of the reputed species of the genus, from the point of view of the structure of the male claspers. In a general way the conclusions suggested show considerable and in some cases remarkable correspondence with the order in which the reputed species have been arranged in existing works. Most of the forms which now appear conspecific have already been placed together as nearly related.

The question of the specific value of the genitalia is difficult and complicated. The claspers have many forms, showing that we are not dealing with a genus in which these organs are of a primitive and simple character. The highly modified form of the armatures in many species supports the view that specific identity alone accounts for the resemblances found between the organs of forms hitherto regarded as distinct. It will be interesting to see to what extent external features help to confirm the conclusions arrived at from anatomical study.

The evidence of pattern and colour.

In considering the question of pattern it is important to distinguish between resemblance due to affinity and that due to mimetic influences, and it is just on this point that the evidence of the genitalia affords valuable clues. Thus the resemblance between "*silvana*" *ethra* and *narcaea flavomaculatus* would at first appear to support the theory of the affinity of *silvana* and *narcaea*. We have seen, however, that whilst on anatomical grounds *silvana* and *narcaea* do appear to be conspecific, "*silvana*" *ethra* is not to be regarded as a *silvana* at all. According to Seitz, *ethra* and *narcaea flavomaculatus* fly together at Bahia and are hardly distinguishable from one another. This fact, coupled with the known anatomical difference, points strongly to an instance of mimetic resemblance. As is well known, most of the Silvaniformes are modified to resemble Melinaeas and other butterflies of different subfamilies. Whether in likeness to a common model or to each other, several forms of the Silvaniformes bear strong resemblance to other Silvaniformes. Thus—

ethilla aërotome	resembles	*pardalinus lucescens.*
anderida melicerta	,,	"*silvana*" *metaphorus.*
anderida zuleika	,,	*hecalisia octavia.*
anderida holocophora	,,	*numatus superioris* (dark form).

In each of these cases, as in that of "*silvana*" *ethra* and *narcaea flavomaculatus*, the forms which resemble one another are *separable on the anatomical structure*, and the resemblance may be regarded as mimetic without stopping to define the particular class of mimicry to which each case should be referred.

Bearing in mind the above facts, we may now consider the extent to which the patterns support the conclusions formed on the anatomy.

The *narcaea* association.

The typical form of this species appears to be very distinct from the other reputed species with which I have associated it, and it cannot be said that pattern affords much support for the conclusions based on the anatomical structure. Other members of the association, however, offer strong support to these conclusions. Comparison of *silvana silvana* with the typical form of *numatus* shows that there is really little difference between their patterns. *H. gradatus thielei* is scarcely separable from forms of *numatus* on pattern. As to *ethilla*, pattern would certainly support the view of a close affinity with *numatus*, especially if the undersides of *numatus numatus* and *ethilla eucomus* be compared. *H. ethilla claudia*, which resembles *anderida melicerta*, stands out rather distinctly from the rest. As we have seen, the claspers of forms of *ethilla* vary greatly, but in *ethilla claudia* they so closely resemble those of *ethilla ethilla* that there can be no doubt of their specific identity. Riffarth's diagnosis of this case was extremely shrewd. With reference to the other reputed species, the claspers of which I have not been able to examine, *H. hippola* must remain very doubtful, though an example of *narcaea satis* with the apical spot suppressed and the discal band darkened to the ground-colour would be difficult to distinguish from *hippola*. It is difficult on mere outward examination to appreciate the grounds on which *sulphureus* has been separated from *ethilla*.

The *novatus* association.

The pattern exhibited by the reputed species here associated are extremely diverse, though some of the special features may be traced through several different forms.

1. A tendency to melanism in the hind-wings is seen in *aristiona* and its forms *messene* and *aurora*, and appears again in *ithaka* and *pardalinus lucescens*, reaching a climax in *hecale* and *anderida fornarina*.

2. The undersides of *aulicus* and *aristiona lenaeus* are nearly identical, if we except the central and marginal black markings of the former, which, however, are traceable as vestiges in the latter.

3. The relationship of the underside pattern of *novatus leopardus* to that of *aristiona arcuella* is very evident on careful comparison.

4. The brown markings seen on the underside of *anderida fornarina* are faintly represented in some examples of *hecale*, whilst the yellow markings of the fore-wing upperside in *fornarina* are partially reproduced in white in *hecale*.

5. Comparison of the hind-wing underside in *pardalinus lucescens* and *aristiona aurora* shows a close relationship of pattern.

6. The pattern of *quitalenus felix* is merely a slight modification of that of *pardalinus tithorides*.

7. The vestigial submarginal yellow spots in the hind-wing of *ithaka* appear to correspond with those in *anderida anetta*.

8. The various *anderida* forms graduate so obviously one into another that a connection between any of them and one of the other reputed species serves as an indirect connection for all.

9. In considering the form of the armature of these species I stated that there was a further reason for connecting "*silvana*" *robigus* with this association. The underside pattern of this form, especially of the hind-wing, is nearly identical with that of *novatus novatus*.

10. The hind-wing underside of *paraensis latus* closely resembles that of *aristiona arcuella*.

11. Similar close resemblances may be observed between examples of *fortunatus* and *pardalinus*.

We thus see that careful comparison of the wing patterns of the *novatus* association tends to support the conclusions based on an examination of the male armatures.

H. vetustus.

This species and its subspecies *metellus*, though closely allied to the *novatus* association, may for the present be kept separate. The forms are rather rare in collections, and I have not been able to examine a large series. It may well prove ultimately to be a member of the *novatus* association.

H. sergestus.

The position of this species is obscure. Its pattern suggests a close relationship with *pardalinus*, but the clasper is of a very different form, and it must for the present remain separate.

H. atthis.

The structure of the armature of this species shows that it belongs to the Silvaniformes, though the pattern has been profoundly modified in mimicry of a *Tithorea*. The markings show no indication of its affinity, though the claspers are hardly distinguishable from those of *anderida*. They are rather less densely tufted.

H. ismenius.

The apparent specific identity of "*silvana*" *metaphorus* with the forms of *ismenius* is one of the surprising results of this investigation. The patterns are very different, though certain similarities may be observed. Thus the white and yellow spots on the underside of the fore-wing apex are practically identical with those in *ismenius telchinia*, and the same may be said of the white spots of the hind-wing underside.

There are two doubtful species included in the Silvaniformes concerning which nothing can be said. They are *H. arcuatus*, Kirby, and *H. euclea*, Godt. Their identity has not been satisfactorily established.

H. tumatumari, Kaye.

This peculiar species has already been mentioned in connection with the armature structure. As stated, the anatomy indicates relationship with *H. vetustus*, and whilst I think there are grounds for regarding it as a good species, certain particulars of the pattern support the above view of its affinity. Examination of the fore-wing underside shows in *tumatumari* three subapical spots and a fourth submarginally placed below the extremity of the first branch of the median. Precisely similar white spots are found in *vetustus metellus*. The discal pattern of the fore-wing evidently bears a close affinity in the two species. If *tumatumari* be carefully examined in a good light, it will be seen that on the hind-wing underside the brown colour above the cell is very dark, whilst beneath this dark area is a paler stripe traversing the cell, its hinder border line passing out of the cell exactly at the origin of the second subcostal branch. The positions of these dark and light areas correspond precisely with those of the black-brown and orange-brown in *vetustus*, whilst there is an orange-brown streak below the cell in *vetustus* corresponding accurately with the distinctive yellow streak in *tumatumari*. Taken singly these points may be small and might be accidental; collectively they appear to me to be very significant.

H. elevatus, Nöld.

It is scarcely surprising that this species has been regarded as a form of *melpomene*. There is practically no external feature to distinguish it, beyond the yellow streak already referred to, yet it is more nearly related to some of the Silvaniformes than to *melpomene*. Three male examples are before me from Chanchamayo, Saõ-Paulo (Amazon), and Beni River (Bolivia) respectively. The first two agree nearly with the description of *elevatus*. The third differs in the following respects. The fore-wing discal yellow fills the outer third of the cell, and extends across the space between the first and second median, and as a suffusion half-way down to the submedian. On the margin of the hind-wing underside it has very distinct white dots, absent in the two other specimens. These dots are described as occurring in the type. In all three the hind-wings above have an orange-red horizontal band passing through the cell and ending beyond the subcostal. This is followed by the usual straight band of black, and seven orange-red internervular "nail-headed" streaks almost reaching the hind-margin.

As has been stated, the armature approaches in structure that of *sergestus*. If there is any real affinity there is no indication of it on the upper surface. On the under surface, when the third specimen described above is compared with *sergestus*, we find that the position and general contour of the fore-wing discal yellow is very similar to that in *sergestus*. The latter furnishes one of the rare cases in which a silvaniform *Heliconius* has a red spot at the base of the hind-wing, and *elevatus* has an exactly similar spot, though, of course, this feature is only of value in conjunction with the anatomical similarity, as so many of the non-silvaniform *Heliconii* have basal red spots.

These two species, *tumatumari* and *elevatus*, are of extraordinary interest as showing that there is no marked line of division between the Silvaniformes and the other members of Section I. The hind-wing pattern of *elevatus* raises another very interesting point. The "flame pattern" so frequently found in *Heliconius* is of two kinds. In *melpomene* forms (Section I) it is always cut across in a nearly straight line and the rays are of the "nail-headed" type, whereas in the species of Section II in which it occurs, the rays at their inner ends follow the contour of the cell. Why should the pattern of *H. elevatus* be of the nail-headed type? The reply seems to me to be that the characteristic horizontal black bar in the hind-wing of species of Section I is an ancestral pattern of considerable stability. It appears in one form or another in *narcaea, silvana, numatus, ethilla, novatus, pardalinus, quitalenus, paraensis, aulicus*, forms of *anderida*, etc., and its inner (upper) edge runs across at the level of the cell end. Hence when a "flame" pattern is developed it is cut off straight along the top by this characteristic bar. Thus, if my suggestion be well founded, we should expect any species of Section I which developed a flame pattern to produce the straight-cut, more or less nail-headed type found in *melpomene* and *elevatus*, irrespective of fascies of more recent ancestry. The nearest approach to a flame pattern in any truly silvaniform-patterned species that I know is in an example before me which agrees with Weymer's *H. fortunatus*. Here the usual black band is very distinct, and beneath it is a series of orange internervular marks of the ground-colour which, whilst running off to fine points marginally, are cut off proximally by the black band and have the nail-head pattern, though greatly foreshortened.

Professor Poulton has suggested to me that the black bar may have been developed in Section I of *Heliconius* in mimicry of *Melinaea* forms, doubtless an association of great antiquity. The idea has much to recommend it, since if it were a character of still greater antiquity we should expect it to be common to both sections of the genus. However that may be, the bar is now a deeply established factor of the pattern, and sufficiently accounts, I think, for the special characteristics of the flame pattern as developed in Section I.

The *melpomene* association.

Some ten reputed species are here included, totalling, with subspecies and varieties, sixty or seventy named forms. On Pl. XI I have figured twenty-six butterflies which exhibit some of the forms included in this association. All the figures are much reduced from natural size, but for convenience of comparison it was desirable to have them all on one plate. The forms of *cydno* exhibit great diversity of pattern. White and lemon-yellow are easily interchangeable in both wings. The broad yellow fore-wing discal band of *cydno* is divided into two separate bands in the form shown at fig. 3, and in fig. 4 there is a submarginal row of white spots, the other fore-wing markings having become white. On the hind-wing of *cydno* there is a white border of medium width, almost marginal. In fig. 3 it is twice as broad, and in fig. 5 it is broad and yellow. In *hermogenes* (fig. 4) it is yellow and considerably separated from the margin, whilst in fig. 7 it is vestigial, but providing a link with the peculiar hind-wing marginal pattern in *vulcanus cythera*, fig. 8. Fig. 2 represents the underside of fig. 1. Note the peculiar pattern of the hind-wing. Two red-brown bands are faintly visible and the white sub-marginal border of the upperside is repeated. In some cases the upper red-brown band is practically horizontal, broad proximally and tapering towards the hind-margin. It is important to bear these variations in mind when comparing the patterns of the other reputed species.

Fig. 14 represents *weymeri*, Stgr., which is separated by Riffarth, but regarded by Seitz as conspecific with *cydno*. The latter view is undoubtedly correct. The fore-wing pattern is only a slight modification of fig. 3, whilst the hind-wing central yellow band is probably a development from the red-brown band of the underside of *cydno*. This central yellow band is a common feature in the genus; it occurs in both sections, and I shall have to refer to it again.

Fig. 15 is the form known as *weymeri gustavi*, Stgr. It has lost the fore-wing markings altogether and become a remarkable mimic of a species in Section II. An example kindly lent me by Mr. Kaye is to some extent intermediate, having in the fore-wing a white spot above the first median, another below the first subcostal, whilst with a lens white scales can be seen in several other positions. The underside of this specimen is very remarkable, since the dull brown colour is paler all round the margin of the hind-wing over an area corresponding exactly with that of the white border in forms of *cydno*. Moreover, on the fore-wing the discal area is paler, not over an area corresponding with the white marks in *weymeri*, but representing the yellow patch of *cydno*.

We may now turn to *heurippa*, a nearly typical example of which is shown at fig. 10. There is little or nothing to associate it with *cydno*. Fig. 9, however, shows the fore-wing of *heurippa* with the *cydno* band in the hind-wing. This is the form known as *wernickei*, Stgr., and there is a somewhat similar form, *emilius*, Weym., which has the hind-wing band slightly suffused with grey as in some forms of *cydno*. These facts would seem remarkable enough, but there is further and stronger evidence. My figs. 10, 11, and 12 show a regular gradation of pattern, ending in the form at fig. 12, which is very near the stage of having nothing but a red patch on the fore-wing. Now this specimen, which is in the Tring Museum, has on the underside (fig. 13) the "ghost" of the pattern of the *cydno* underside. The delicacy of the shades of brown is difficult to reproduce, but the beauty of the actual specimen is very striking, and I am certain that no one could see it without being convinced of the specific identity of *cydno* and *heurippa*. The specimen shown at fig. 11 is also remarkable from the fact that on the underside of the hind-wing there is a pale horizontal band exactly corresponding to the yellow horizontal band of *weymeri*.

At fig. 16 is a figure of a form of *melpomene* which does not quite correspond with any of those named in the monograph already referred to. The fore-wing has the bicoloured patch of *heurippa*, but in other respects the example resembles *melpomene amandus*, shown at fig. 17. This form approaches *nanna burchelli*, but has more red in the cell. *H. melpomene amandus*, fig. 17, connects *nanna* with *heurippa*, and through the latter with *cydno*. Fig. 18 is *amaryllis rosina*, which is merely a form of *melpomene* with the hind-wing yellow band, whilst fig. 19

is *amaryllis euryades*, lacking the yellow band on both surfaces of the hind-wing, though in the form *euryas* it is present on the underside, and in one example before me from the Rio Dagua there is a trace of a white submarginal band on the hind-wing underside. These forms bring us to *melpomene*, fig. 20, which is merely a modification of the form of *heurippa* shown at fig. 12. All the yellow has disappeared and nothing but the bright red fore-wing patch remains. Occasionally an example of *melpomene* may be found in which the dull brown of the hind-wing underside has a rather lighter appearance corresponding in position to the yellow band of other forms.

Fig. 21 is the form described by Lathy as *xenoclea confluens*. It may be regarded either as a *xenoclea* in which the two patches have run together, or more probably as a *melpomene* with an extended patch not yet separated into two. In any case it connects *melpomene* with *xenoclea*, shown at fig. 22. In fig. 23 the two patches of *xenoclea* are white with a dusting of red. The example shown at fig. 24 exhibits the well-known "flame" pattern in the hind-wings together with basal red in the fore-wing. The flame pattern occurs in many forms of *melpomene* and also in species of Section II, though in the latter the red streaks radiate from the borders of the cell and have not the appearance of being horizontally cut off at their upper end.

Fig. 25 represents *melpomene eulalia*, in which, as in fig. 26, we see a distinct trace of the *heurippa* band in the fore-wing, the flame pattern recurring in fig. 26. Fig. 27 is a remarkable combination of the *melpomene amandus* fascies with the flame pattern superimposed. Finally, fig. 28 shows *H. pachinus*. The genitalia of this cannot be distinguished from those of all the other forms shown on the plate, and as to pattern, the yellow bands appear to be a mere modification of those of the fore-wing of figs. 3 and 6 and the hind-wing of fig. 4. Moreover, on the underside of *pachinus* there is frequently to be seen on the hind-wing a submarginal series of white spots like the vestige of the white border of *cydno*.

I have discussed the *melpomene* association at some length because I happen to have had access to a great number of examples, and these fortunately exhibit remarkable intermediate forms, which, together with the preparations of genitalia, provide, at least in my own opinion, conclusive evidence of the specific identity of all the forms above considered, and divided in Stichel and Riffarth's monograph into ten species. Considered alone, the question of whether all these forms are representatives of one or several species is of little real importance except as a study in variation. The interest of the matter will, however, become apparent when we come to investigate the peculiar mimetic relationships occurring between the two sections of the genus.

H. besckei.

This species I keep separate both on account of the form of the clasper with its tuft of bristles and also because of the pattern of the hind-wing underside. Kaye was at one time of the opinion that it was a form of *erato phyllis*, though this cannot be maintained in view of the structure of the male claspers. Also I think it is rightly placed in Section I. It should be noted, however, that on the hind-wing underside there are some small whitish spots at the apex, and similar spots are occasionally found in examples of *melpomene*, and the relationship, if not specific, is extremely close.

SECTION II.

H. crispus.

I have not been able to examine the armature of this species, and the pattern, being so profoundly modified in mimicry of a *Tithorea*, furnishes little evidence of its identity.

H. hecuba.

The patterns of *hecuba*, *choarinus*, and *cassandra* support the view that they are all one species, and whilst I have had no example of *longarenus* to examine, its pattern indicates that it is conspecific with *cassandra*. If another example of *longarenus* is ever discovered I shall be surprised if its locality is not found to be identical with that of *gynaesius*.

H. hecalesia.

The armature of *hecalesia* is so characteristic that the fact of the same organ in *octavia* being precisely similar leaves no doubt in my mind that they are forms of the same species. An examination of pattern leaves little doubt that *gynaesius* is also a form of *hecalesia*, since *octavia* forms an almost perfect transition thereto. Indeed, if the basal brown be eliminated from the fore-wing of *octavia* there is no distinction from that of *gynaesius*, whilst a proportionate reduction of the hind-wing brown in *octavia* would leave the hind-wing pattern of *gynaesius*. If Stichel and Riffarth were satisfied that *gynaesius* was a form of *hecalesia* it is strange they should have kept *octavia* separate. It should further be noted that whilst the underside of the hind-wing in *octavia* has a very different appearance from that in *hecalesia*, it is practically identical with that in *hecalesia formosus*, whilst the latter has a trace of the fore-wing basal brown found in *octavia*.

H. godmani.

Stichel and Riffarth place this form in their Aoediformes, presumably on account of its shape. In other respects it differs little in appearance from *gynaesius*. The structure of the armature would probably settle the point at once, but I know of no example except the type, and this is not available for dissection.

H. metharme.

Whilst the difficulty of distinguishing the claspers suggests the specific identity of *metharme* and *aoede*, the difference in the shape of the wings suggests their separation. On the other hand, the radiate red pattern in the hind-wing in *aoede* is repeated on the underside of *metharme*, and there is an example of the latter in the Tring collection, having indications of the flame pattern on the upperside, though it must be remembered that the radiate pattern is common in several undoubtedly separate species. I think we must be content to regard them as doubtful species, but certainly very nearly allied.

H. xanthocles, H. hierax, H. egeria.

These three species are sufficiently distinct on the structure of the armature, and need no further comment.

H. burneyi.

The suggestion that *burneyi* and *wallacei* are conspecific is strongly supported by their patterns. On the hind-wing underside the white internervular streaks and fringes are well represented in *wallacei colon*, the peculiar arrangement of the basal red is similar, and the conspicuous precostal yellowish spot is common to both. The base of the fore-wing costa beneath in *wallacei* is deep red, corresponding with a more conspicuous basal red in *burneyi*. Indeed, the hind-wing undersides in *wallacei colon* and *burneyi catharinae* are practically identical, and if a series of the hind-wings of both were mixed together it is difficult to see on what grounds they could be separated.

H. doris.

This species and its forms are readily recognised and specifically distinct, as the male claspers show, though many features of the pattern would suggest relationship with *metharme*.

H. hewitsoni.

A distinct species, as shown by the armature.

H. congener.

Probably distinct, on the structure of the armature.

H. sapho, etc.

The forms of *sapho* resemble those of *cydno*, and, as in that species, the two colours, lemon-yellow and white, are remarkably interchangeable. The broad white discal band in *sapho eleusinus* and *sapho leuce* appears as a double yellow band in several other forms, whilst the hind-wing hind-marginal white may vary from a mere fringe in *sapho leuce* to a broad band in *eleuchia*, or become a still broader yellow band in *sapho primularis*. The reputed species *antiochus*, *leucadia*, and *sara* do not show any characteristic differences in the structure of the claspers, and their patterns support the theory of specific identity in the following ways—

1. All have a tendency to white fringes pointed with black at the nervure ends.
2. The fore-wing subcostal and median nervures are generally dusted with pale yellow on the underside, the fore-wing subcostal almost invariably. In *antiochus* this dusting is on the subcostal and median. In many species of *sara* and *leucadia* the yellow scales can be seen on the median with a lens.

3. A very slight modification of the two fore-wing yellow bars in *sapho eleuchia* gives us the characteristic yellow or white bars in forms of *antiochus*.

4. *H. sara theudela* presents only a very slight modification of the pattern of some examples of *sapho primularis*.

5. Some examples of *leucadia pseudorhea* have the rudiments of a hind-wing marginal white border, strongly suggesting that more highly developed in *theudela* and forms of *sapho*.

6. Many forms of *leucadia* and *sara* have on the underside of the hind-wing a variable number of red spots forming a discal row more or less parallel with the hind-margin, though I have not seen any trace of this in *sapho* or *antiochus*.

7. Except for the red subcostal streak in *antiochus*, the hind-wing basal spots on underside of that species are almost exactly like those in *sara*. Moreover, in many examples of *antiochus* there is a yellow spot near the middle of the inner margin on the hind-wing underside. Several specimens of *sara* show the same peculiar yellow spot.

H. erato, etc.

The forms and reputed species included in this association present a case somewhat analogous to the great *melpomene* association in Section I.

The following considerations of the patterns support the conclusions based on the structure of the armatures—

1. *himera* may well be a form of *hydarus* with the red and yellow markings reversed.

2. *notabilis microclea*, with its double spots, may be traced to *erato* through a form of *erato estrella*, which has white subapical spots in the fore-wing, exactly the same white spot appearing in *notabilis notabilis*.

3. *hydarus hydarus* (resembling *melpomene*) has several admittedly conspecific forms which are totally unlike. Of these *hydarus colombinus* has a red fore-wing discal band and a central horizontal hind-wing yellow band. Beyond a slight difference in shape of this yellow band there is little to distinguish it from that of *petiveranus*.

4. *hydarus chestertoni* is a glossy blue form with a central horizontal hind-wing yellow band. If *cyrbia* be compared with this, the hind-wing yellow in that form, apparent only on the underside, is quite evidently the same as that

in *hydarus chestertoni*, *cyrbia's* fore-wing red being obtained from *hydarus hydarus*. The peculiar white-dusted hind-wing border in *cyrbia* is more difficult to account for. It would at first suggest affinity with *sapho*, but the structure of the armature precludes this. The form is, of course, either a mimic or a model of *vulcanus cythera*.

5. *amphitrite* is merely a development of *hydarus*, the armatures being practically identical.

6. *erato* appears in many forms, some of which have developed the flame pattern common in other species. All kinds of intermediates are known, for which some forty-three names are recorded by Seitz. Most of these forms resemble others belonging to Section I, of which they are either the models or mimics. Its variability is, perhaps, even greater than that of *melpomene*, and there is nothing improbable in supposing that the forms I have associated with it are really the same species.

H. hermathena.

Closely related to the *erato* association, but apparently distinct. A very remarkable species combining the fore-wing spots of *erato phyllis* with the hind-wing of *charithonia*.

H. charithonia.

The true relationship of this common form is rather obscure. It is apparently a good species.

H. nattereri, H. fruhstorferi.

Of these I have had no examples to examine. There is, as already stated, some probability that they are male and female of the same species, though whether distinct or merely forms of *charithonia* must remain for the present undecided.

H. clysonimus, H. hortense, H. telesiphe.

These three forms are probably distinct species and call for no special comment, except that *clysonimus* is probably related to *antiochus* through forms of *sara*, in which traces of the hind-wing red band can still be seen.

We thus see that examination of the patterns and colours of the various forms dealt with supports in most cases the relationships suggested by the study of the genital armatures. We may, therefore, draw up the following table embodying the results of the foregoing investigation. Forms apparently not specifically distinguished are placed under one number. Those forms, examples of which have not been available for examination, are marked with an asterisk. Except where otherwise stated, all the subspecies formerly included under a type name are here included also.

SECTION I.

1. *H. narcaea*, Godt.
   ,, *numatus*, Cram.
   ,, *silvana*, Cram. (not including *metaphorus*, *robigus*, and *ethra*).
   ,, *ethilla*, Godt.
   ,, *gradatus*, Weym.
   ,, *sulphureus*,* Weym.
   ,, *hippola*,* Hew. (?)
2. *H. novatus*, Bates (including *schultzei*, Riff.).
   ,, *hecale*, Fab.
   ,, *aristiona*, Hew.
   ,, *ithaka*, Feld.
   ,, *pardalinus*, Bates.
   ,, *fortunatus*, Weym.
   ,, *quitalenus*, Hew.
   ,, *anderida*, Hew.
   ,, *paraensis*, Riff.
   ,, *aulicus*, Weym.
   ,, *ennius*,* Weym. (?)
   ,, "*silvana*," *robigus*, (?) Weym.
   ,, ,, *ethra*, (?)
3. *H. atthis*, Doubl.
4. *H. vetustus*, Butl.
5. *H. tumatumari*, Kaye.
6. *H. sergestus*, Weym.
7. *H. elevatus*, Nöld.
8. *H. ismenius*, Latr.
   ,, "*silvana*," *metaphorus*.
9. *H. cydno*, Doubl.
   ,, *weymeri*, Stgr.
   ,, *pachinus*, Salv.
   ,, *melpomene*, Linn.
   ,, *heurippa*, Hew. (including *rubellius*, Gr.-Sm.).
   ,, *amaryllis*, Feld.
   ,, *vulcanus*, Butl.
   ,, *xenoclea*, Hew.
   ,, *nanna*, Stich.
10. *H. besckei*, Ménétr.

SECTION II.

11. *H. crispus*, Stgr.
12. *H. hecuba*, Hew.
,, *choarinus*, Hew.
,, *cassandra*,* Feld.
,, *longarenus*,* Hew.
13. *H. xanthocles*, Bates.
14. *H. hierax*, Cram.
15. *H. hecalesia*, Hew.
,, *octavia*,* Bates.
16. *H. godmani*, (?) Stgr.
17. *H. metharne*, Erich. } (doubtfully separate).
18. *H. aoede*, Hübn.
19. *H. egeria*, Cram.
20. *H. burneyi*, Hübn.
,, *wallacei*, Reak.
21. *H. doris*, Linn.
22. *H. hewitsoni*, Stgr.
23. *H. congener*, Weym.
24. *H. sapho*, Dru.
,, *antiochus*, Linn.
,, *leucadia*, Bates.
,, *sara*, Fab.
25. *H. himera*, Hew.
,, *notabilis*, Godm.
,, *cyrbia*, Godt.
,, *favorinus*, Hopf.
,, *petiveranus*, Doubl.
,, *hydarus*, Hew.
,, *erato*, Linn.
,, *amphitrite*, Riff.
26. *H. hermathena*, Hew.
27. *H. charithonia*, Linn.
28. *H. nattereri*,* Feld. } ? ♂ and ♀.
,, *fruhstorferi*,* Riff.
29. *H. clysonimus*, Latr.
30. *H. hortense*, Guér.
31. *H. telesiphe*, Doubl.

One fact is especially striking. If the conclusions arrived at are sound, Section I, containing some 35 reputed species, is reduced to 10, whilst Section II, containing some 37 reputed species, is reduced to 21. Furthermore, when considering the mimetic side of the question, it will appear

TABLE I.—Forms of *Heliconius* and those of other genera which they resemble.

Heliconius	Spp. of other genera	Locality
narcaea narcaea "silvana" ethra	Mechanitis nessæa lysimnia, Hübn. Ceratinia daeta, Boisd. Melinaea ethra, Godt. Dismorphia astynome, Dalm.	Central Brazil.
narcaea connexa	Ceratinia euryanassa, Feld. ? Eresia eunice, Hübn.	S. Brazil.
numatus numatus	Hirsutis harmonia, Cram. Lycorea ceres, Cram. Melinaea mediatrix, Weym. Mechanitis pannifera, Butl.	Br. Guiana.
numatus isabellinus ? aristiona arcuella quitalenus sisyphus	Melinaea flavosignata phasiana, Butl. ? Lycorea eva concolor, Staud. Ceratinia maenas, B. Haas.	W. Amazon.
silvana silvana	Melinaea paraiya, Reak. Mechanitis silvanoides, Godm.	Guiana, etc.
ethilla ethilla	Protogonius ochraceus, Butl. Hirsutis megara, Godt.	Trinidad.
ethilla metalilis	Hirsutis furia, Godm.	Venezuela.
ethilla aërotome pardalinus lucescens	Lycorea cleobaea cinnamomea, Weym. Melinaea maelus cydon, Godm. ,, madeira, Staud. Mechanitis equicoloides, Godm. ,, egaënsis, Butl. Ceratinia pardalina, Hopf. ,, fluonia, Hew.! ,, anastina, Bates Dismorphia egaëna, Bates Protogonius castaneus, Butl.	W. Amazon.
ethilla claudia "silvana" metaphorus anderida melicerta	Melinaea idae, Feld. Mechanitis macrinus, Hew. Callithomia beronilla, Hew. Ceratinia philetaera, Hew. Ithomia iphianassa panamensis, Bates	Panama, Colombia, Ecuador, etc.
aristiona aristiona	Mechanitis deceptus, Butl. Melinaea mothone, Hew. Ceratinia honesta bicolora, Hsch. ,, manaos semifulva, Salv. Napeogenes achaea, Hew. Hyposcada fallax, Staud. Eresia murena, Staud. ,, ithomiola, Salv. Protogonius semifulvus, Butl. Eueides acacetes, Hew. Papilio bachus, Feld. Pericopis hydra, Butl. Castnia pellonia, Druce	*Bolivia, Peru.*

aristiona messene	Melinaea messenina, Feld. Mechanitis messenoides, Feld.	Colombia, Ecuador.
aristiona lenaeus	Melinaea zaneka, Butl.	Ecuador.
aristiona tarapotensis	Melinaea menophilus tarapotensis, Haen.	Ecuador.
aristiona euphone	Melinaea menophilus menophilus, Hew.	Colombia.
aristiona aurora	Melinaea lucifer, Bates Ceratinia soror, Srkr.	W. Amazon.
aristiona timaeus	Melinaea flavosignata orestes, Salv.	W. Amazon.
anderida zuleika hecalesia octavia	Hirsutis pinthias, Godm. ,, duenna, Bates ? Phyciodes ithomoides, Hew. Ceratinia *callispila*, Bates Napeogenes tolosa, Hew. Callithomia hedila, Godm. ,, *hezia*, Hew. Hyposcada adelphina, Bates Eresia nigripennis, Godm.	Central America.
atthis charithonia peruvianus	Tithorea pavonii, Butl.	Peru.
ismenius ismenius	Melinaea messatis, Hew. Napeogenes larina, Hew. Hyposcada adelphina, Bates Ithomia candescens, H.-Sch.	Colombia.
ismenius faunus	Ithomia celemia, Hew. Ceratinia fulminans, Hew.	W. Colombia.
ismenius clarescens	Melinaea scylax, Salv. Ithomia plaginota, Butl. ,, callipsila, Bates. Dismorphia sororna, Butl. (♀)	Costa Rica, etc.
ismenius telchinia	Melinaea imitata, Bates Lycorea atergatis, Doubl. Mechanitis doryssus, Bates Eueides cleobaea zorcaon, Reak. Ceratinia dionaea, Hew. Perrhybris malenka, Hew. (♀) Dismorphia praxinoe, Doubl. (♀) Eresia philyra, Hew. (♀) Protogonius cecrops, Doubl. Pericopis angulosa, Walk.	Central America.

that all but two species in Section I mimic species of other genera. Intrageneric mimicry occurs between two or three species in Section I and between a much larger number of species in Section II. One species in Section I produces forms which mimic six or seven species in Section II, a phenomenon recalling that of the mimicry of several species of *Planema* by one species of *Pseudacraea.*

Whilst I think that fuller knowledge of the genus is likely to confirm the majority of the conclusions here attained, it must not be forgotten that cases occur in which Lepidoptera quite undistinguishable on the armature structure are, nevertheless, known from other characters to be distinct species, and it seems probable that instances of this condition will also be found in the present genus.

The mimetic relationships of *Heliconius.*

The species and forms included under the group Silvaniformes nearly all resemble species of other genera and subfamilies. They are members of great mimetic associations which include species of widely separate affinities. It is not within the scope of the present paper to study in detail all these associations. They are fairly well known, and have been referred to by many authors. Beyond the fact that *hecalesia octavia* resembles *anderida zuleika*, the forms of Silvaniformes, excluding the intermediate *tumatumari* and *elevatus*, do not, as a rule, resemble those of members of Section II of the genus. The accompanying table (Table I) gives some of the more striking associations to which forms of the Silvaniformes belong.

As already stated, Mr. W. J. Kaye has pointed out* that, having once separated the forms of the genus into their two sections, we find that many of those of Section I resemble forms of Section II. In order more fully to illustrate this remarkable parallelism, I have prepared Pl. XII. The figures, as in Pl. XI, are much reduced, but will suffice to illustrate the patterns. The examples shown in the second and fourth columns are all forms belonging to *melpomene*—that is, accepting the conclusions already arrived at, are all the same species. The specimens figured in the first and third columns are all members of Section II, and belong to several species.

Fig. 1 is *egeria egerides*, fig. 2 *melpomene funebris cybele.*

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* *Loc. cit.*

Both occur in Guiana and North Brazil as far as the Rio Negro. Figs. 5 and 6 are *burneyi hübneri* and *melpomene penelope*, both from Bolivia. Figs. 9 and 10 represent *hewitsoni* and *pachinus* from Panama. Figs. 13 and 14, 17 and 18, 21 and 22 represent respectively three forms of *sapho* and three of *cydno*. Figs. 25 and 26 are *himera* and *melpomene timareta contiguus*. In this case the patterns are by no means so alike as in most of the other examples, but that of the hind-wing of the *melpomene* form is the more interesting in that it shows the crowding together of the flame pattern rays in order to produce a resemblance to the band of *himera*.

Figs. 3 and 4 are *notabilis microclea* and *xenoclea* respectively, and beneath them (figs. 7 and 11) are *notabilis notabilis* and *erato rothschildi*, to which correspond the two *melpomene* forms, figs. 8 and 12. Figs. 15 and 16 are *hydarus chestertoni* and *weymeri gustavi*. These, I am told, have not the same vertical distribution, though possibly their enemies may not be correspondingly separated. Figs. 19 and 20 are *hydarus colombinus* and *amaryllis rosina* from Bogota. Figs. 23 and 24 represent *erato phyllis* and *melpomene amandus*, the latter example approximating to the form *nanna burchelli*, Poulton. It has been pointed out by Professor Poulton (Ann. Mag. Nat. Hist., p. 33 et seq., 1910) that where *nanna* occurs within the range of *erato phyllis* the red bar of the fore-wing is deeply toothed at the lower outer edge, just as in *erato phyllis*, whereas in his form *burchelli* the red bar is of less irregular outline. Finally, at figs. 27 and 28 are shown peculiar forms of *erato* and *melpomene* from Bolivia.

Adhering to our previous conclusions, we have, then, on Pl. XII, fourteen forms of *one* species of Section I which, whilst differing widely from one another, present respectively a remarkable resemblance to fourteen forms of Section II belonging to *six* different species. The examples shown by no means exhaust the subject. It would be possible to fill another plate with corresponding forms of *erato* and *melpomene*; *aoede, xanthocles* and *doris*, all have forms which could be included, and whilst so many forms in Section I mimic others in Section II, some of those in the latter seem to mimic each other. The nature of this mimicry is somewhat difficult to define. Mr. Kaye (*loc. cit.*) has himself pointed out its peculiarities. The comparative rarity of the forms of Sections I and II is not constant.

Thus *nanna* and *rosina* are much rarer than *phyllis* and *colombinus*, whilst, on the other hand, *xenoclea* is much commoner than *notabilis microclea*. He points out, however, the possibility that in some or, perhaps, most of the localities, members of one section may be always more dominant than the other. Also that the exact times of appearance may not coincide.

Hitherto it has been the custom to assign all such cases of mimicry either to the Batesian or Müllerian category. Those of us who have heard Mr. Swynnerton's remarks on his experiments in South Africa, given some time ago before the Linnean and Entomological Societies, know that the relative distastefulness of insects is a variable character dependent on factors not entirely related to the insect itself. Mr. Swynnerton's papers are not yet published, so that I cannot utilise his results for the present discussion. Meanwhile, we know that, although no direct experiments have been made with *Heliconius*, the genus gives great evidence of being a distasteful one, and we may therefore regard the existing resemblances as being of a Müllerian character. We are, however, faced with the difficulty of the multiplicity of patterns. If Section II contains the models it would appear to be a great disadvantage to the forms to have so many different appearances, since each form is not necessarily confined to a special locality but considerable overlapping occurs. Where mimicry occurs between separate species of separate genera, then multiplicity of patterns in the models may be compensated for by diversity of habit of the different species. Thus Mr. Kaye, in discussing mimetic groups in the Potaro district of British Guiana, states that the species of *Heliconius* with patterns resembling *Ithomiinae* frequent flowers of a certain plant, whilst other species of *Heliconius* are never, in his experience, found on these flowers. This is an extremely valuable point and one which should be remembered in considering mimetic phenomena.

It does not, however, seem probable that forms of the same species will have different habits corresponding to those of their respective models. Apart from the preferences of insectivorous enemies, whether absolute or conditional, the unpalatability of the insect is, of course, a relative factor. Thus resemblance of a species of *Heliconius* in Section I to a species in Section II may be a measure of protection to both, assuming the two species to possess a certain degree of distastefulness. Another species of *Heliconius* may resemble a *Melinaea* or a *Lycorea*. We know that in most cases the Melinaeas are much more numerous than *Heliconius*, and we may suppose that the former are so much more unpalatable than the latter that, in spite of the degree of distastefulness in *Heliconius*, the latter may be practically a Batesian mimic of the *Melinaea*. At the same time it is, perhaps, inappropriate to use the term Batesian in this connection, since it was the mimicry of *Heliconius* which Bates himself felt unable to explain on his own theory. To understand more fully the relationships of models to mimics in *Heliconius* we require much more information concerning geographical distribution, and also as to comparative rarity of forms and other bionomic factors. S. America is a very large area, and the commonest type of data on our labels is "Upper Amazon," "Colombia," "Peru," and even sometimes "Brazil." We might as well be told that a certain insect occurs in Europe.

Including the examples figured on Pl. XII the following is a list of some of the most remarkable instances of intrageneric mimicry in the genus.

SECTION I.	SECTION II.
cydno chioneus	*sapho eleusinus*
,, *epicydnides*	,, *eleuchia*
,, *galanthus*	,, *leuce*
,, *alithea*	,, *primularis*
weymeri gustavi	*hydarus chestertoni*
pachinus	*hewitsoni*
melpomene funebris cybele	*xanthocles*
,, *equadoriensis*	,, *melior*
,, *vicinus*	,, *melete*
,, *funebris deinea*	*burneyi catharinae*
,, *penelope*	,, *hübneri*
,, *penelope margarita* (?)	*erato anacreon ottonis*
,, *timareta contiguus*	*himera*
,, *aglaope* f.	*erato rothschildi*
xenoclea corona	*notabilis notabilis*
amaryllis rosina	*hydarus colombinus*
,, *euryades*	,, *hydarus*
vulcanus cythaera	*cyrbia cyrbia*
xenoclea	*notabilis microclea*
nanna nanna	*erato phyllis*

SECTION II.

doris delila	*burneyi hübneri*
,, *metharmina*	*metharme* *sara* ff.

Of the genus *Eueides*, Seitz remarks that it may be said that no *Eueides*, without any exception, has a character of its own. Some copy *Heliconius*, others *Lycorea* and *Actinote*, and in some species the male copies one species whilst the female resembles another. A few of such resemblances are given below.

Eueides.	Heliconius.
ricini, Linn. *procula*, Doubl.	*clysonimus* *hortense*
eanes, Hew.	*erato lativitta*
eanes eanides, Stich.	*melpomene aglaope* f.
dianasa, Hübn.	*narcaea*
,, *decolorata*, Stich.	,, *satis*

All the numerous forms of *E. isabella*, Cram., resemble various forms of *Heliconius* of the Silvaniformes group.

In addition to the mimetic associations above tabulated there are further instances of considerable interest. Thus the resemblance of *Colaenis telesiphe* to *H. telesiphe* is well known. They fly together and cannot be distinguished on the wing. In Ecuador the *Heliconius* has the hind-wing band yellow instead of white and broader than in the typical form. The *Colaenis* in the same region is correspondingly modified. Several Papilios present Heliconoid patterns, notably *P. zagreus*, Doubl., and its form *P. bachus*, Feld., which have an appearance recalling that of species of the Silvaniformes. *P. pausanias* is a mimic of *H. sara* and is also said to imitate the *Heliconius* flight.

P. euterpinus, Godm., though it can only be said to be a rough mimic of a *Heliconius*, presents the *melpomene* pattern which, as Dr. Dixey has shown, may be traced over a large area and through many species, including many forms of *Heliconius*, *Eresia castilla*, Feld. *Adelpha lara*, Hew., *Agrais amydon*, Hew., *Siderone* spp., *Catagramma euomia*, Hew., *Callithea davisii*, Butl., *Daedalma* sp., several species of *Pereute*, *Catasticta tentamis*, Hew., and a number of moths, including Arctiids, Hypsids and Syntomids. With regard to *H. erato phyllis*, Seitz (Macrolepidoptera) records that, whilst it occurs all the year round in Rio and Santos, it becomes comparatively scarce in January and February, at which season only worn specimens are found. At the same time *Eresia lansdorfi* appears, a species which, as may be seen from its pattern, copies not a fresh, but a worn and faded *phyllis.* Several forms of *Heliconius* resemble species of *Tithorea* and *Hirsutis.* Some have already been mentioned, as *H. atthis*, etc. *H. crispus* flies with *T. bonplandii descandollesi* in the Cauca Valley. *H. hecuba* mimics *T. humboldti*, and *H. hecuba tolima* is a copy of *T. bonplandii. H. hecalesia* resembles *T. hecalesina*, *Ceratinia peridia*, *Callithomia tridactyla*, and others which form a large association, whilst its Central American form, *formosus*, resembles *T. pinthias.*

It is remarkable that *H. charithonia*, perhaps the commonest species of *Heliconius*, should have no close imitators. Professor Poulton points out to me that the females of *Catonephele nyctimus* approach this pattern, as also do those of *C. acontius.* The latter has a wider eastward range than *charithonia*, but the former is the better mimic in that the hind-wing yellow band is broader, though in both cases the resemblance is very slight. The *peruvianus* form of *charithonia* is evidently a modification in the direction of *Tithorea pavonii*, Butl., the marginal and submarginal spots being white instead of yellow. In one respect it is a better mimic of the *Tithorea* than is *H. atthis*, since the fore-wing yellow band is broader, as in the *Tithorea*, and curves down, not up, as in *Atthis.* The ♀ of *Pieris viardi*, Boisd., is also modified in the direction of *H. charithonia*, whilst *P. mandela tithoreides*, Butl., approaches *Tithorea pavonii* in the same way as does *H. charithonia peruvianus.*

Some of the most interesting *Heliconius* mimics occur amongst the *Pierinae*, such cases being the more noticeable since the normal Pierine fascies are so unlike those of *Heliconius.* Thus, *Euterpe bellona hyrnetho*, Fruhst., ♀, from Bolivia, has black wings with a fore-wing discal yellowish patch and a radiate red pattern on the hind-wing, thus resembling similar forms of *H. erato. Euterpe bellona cutila*, Fruhst., ♀, also shows the incipient stages of such a pattern. *E. bellona negrina*, Feld., ♀, bears on the underside a very good copy of the underside of *H. erato venusta.*

It is interesting to note that the flame pattern in these Pierines is a copy of that occurring in the species of *Heliconius* belonging to Section II, and not those of Section I. *Pieris mandela locusta*, Feld., ♀, and the form *noctipennis* resemble to some extent *H. sapho leuce*, whilst *Pereute charops*, Boisd., ♀, resembles *H. hydarus*. On the underside of the hind-wing (all that shows when at rest) the female of *Perrhybris lorena* is very like *H. antiochus aranea*, though the upperside is more like one of the Silvaniformes. A similar silvaniform appearance is also presented by several females of *Perrhybris*, though the resemblance is probably secondary, both being influenced by Ithomiine models. It seems unnecessary further to enumerate special cases of mimicry connected with the genus. An examination of any large collection will convince the observer of the prevalence of mimetic patterns.

Apart from a few exceptional instances, it appears to be the rule that, whereas species of *Heliconius* belonging to Section I are mimetic and constitute members of large associations of which they are not themselves the dominant models, species of Section II act as models and are imitated either by forms of Section I or by butterflies of other genera, and moths. The *melpomene* forms of Section I seem to be all one species, whereas their counterparts in Section II belong to several. Again, where a butterfly of another genus appears to be a *Heliconius* mimic, its model will almost always be found in Section II and not in Section I. Thus *Eueides* finds its models in Section II. Even *Napeogenes duessa* is apparently an incipient mimic of an *erato* form which is very perfectly imitated by a moth of the genus *Pericopis*. Moths of this genus come into mimetic associations of which silvaniform *Heliconii* are fellow members, but the moths are certainly not the models, though *Pericopis* is doubtless a protected genus. Distastefulness is a relative factor, and we are, of course, quite justified in speaking of model and mimic, even in Müllerian associations. The model is the form which, from whatever cause, not necessarily palatability, has attained to a greater predominance, and in the genus *Heliconius* it would appear that, generally, the species of Section II have in some way evolved a degree of such predominance superior to that enjoyed by the species of the other half of the genus. It is interesting to see an independent property of this kind correlated with recognisable differences of internal anatomy and a slight, though evident, external characteristic.

It remains to consider certain points in connection with the modifications which occur in various geographical areas. Several exhibits have been made and papers read on this subject. Mr. W. J. Kaye read a paper in 1906,* in which he described and illustrated the many forms of *Melinaea*, *Heliconius*, etc., forming a great characteristic group in the Potaro District of British Guiana. In this group were found to occur the following forms :—

NYMPHALIDAE.
    Ithomiinae.
        Melinaea 4
        Mechanitis 2
        Ceratinia 2
    Heliconinae
        Heliconius 4
        Eueides 3
    Nymphalinae
        Eresia 1
DANAIDAE
    Lycoreanae
        Lycorea 2
ERYCINIDAE
    Lemoniinae
        Stalachtis 1

together with the outlying members of the group not up to that time actually taken on the Potaro, *Tithorea harmonia*, Cram., *Protogonius hippona*, Cram., *Dismorphia amphione.*

The dominant member of the group was *Melinaea mneme*, Linn., which occurred in "prodigious numbers." The *Heliconius* forms were found to be by far the closest mimics of the *Melinaea*, whilst at the same time they were comparatively rare.† Great variation was observed in the banding of the hind-wing from a narrow bar to almost entirely black. A careful and interesting analysis is made of the degree of blackening observed in the various forms, with the result that there is found to be a closer agreement on the underside than on the upper. Only two species showed a large proportion with heavy black underside. The tendency to melanism was found to be more prominent on the upperside. The author concludes that the forces of selection are now acting more forcibly on the underside pattern, as might be expected from the sedentary habits of the group, and that these forces are now tending to produce forms with less blackening. A further point of great interest was that already mentioned—namely, that all the members of the group are commonly found feeding on the white flowers of *Eupatorium macrophyllum*, and that whilst there are many other differently coloured forms of *Heliconius* in the neighbourhood, they are never, in the author's experience, found on these flowers. This point is worthy of special remark as showing how the advantages of similarity of pattern may be increased by the development of a common habit.

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* Notes on the dominant Müllerian group of butterflies from the Potaro District of British Guiana. Trans. Ent. Soc. Lond., p. 411 et seq., 1906.

† See also Proc. Ent. Soc., p. liv, 1903.

In 1908 Mr. J. C. Moulton read a paper "On some of the principal Mimetic (Müllerian) Combinations of Tropical American Butterflies" (Trans. Ent. Soc., p. 585 et seq., 1908) in which he described four great associations of mimetic forms, including *Ithomiinae*, *Heliconinae*, and members of other subfamilies. Association I is classed as the North Central American type from Guatemala, Honduras, and Nicaragua. The typical pattern is here that of *Melinaea imitata*, which is closely copied by *H. ismenius telchinia*, the rest of the group including—

Ithomiinae	5
Danainae	1
Nymphalinae	2
Heliconinae	1
Pierinae	2
Hypsidae	1

Association II is described as the East Brazilian type and is divided into two subgroups (*a*) having the fore-wing subapical spots yellow and (*b*) having the same spots white. The first is centred round *Melinaea ethra*, Godt., and includes *H.* "*silvana*" *ethra* and other species of the following subfamilies :—

Ithomiinae	4
Danainae	1
Nymphalinae	2
Heliconinae	1
Pierinae	1

Table II.

	Guiana			Venezuela	Colombia	Central America	Ecuador	Peru	Bolivia	E. Amazon	W. Amazon	E. Brazil	S. Brazil	Trinidad
	French.	Dutch	British									(S. of Amazon)		
I. *melpomene* pattern. Black with f.-w. red patch	melpomene	melpomene	melpomene vulcanus pyrforus	amaryllis rosina euryas amaryllis euryades	amaryllis rosina euryas vulcanus	amaryllis rosina euryas vulcanus	melpomene	melpomene amaryllis euryades		melpomene				amaryllis euryades
		erato callycopsis		hydarus hydarus guarica	hydarus hydarus guarica	hydarus petiveranus tristis		amphitrite		erato callycopsis				hydarus
II. *huebneri* pattern. F.-w. with basal red and discal yellow H.-w. with "flame" pattern	melpomene eulalia	melpomene eulalia					melpomene aglaope	melpomene aglaope	melpomene penelope	melpomene thelxiope melpomene aglaope	melpomene aglaope			
	aoede xanthocles vala doris delila	xanthocles vala doris delila		aoede lucretius	xanthocles melete		aoede bartletti xanthocles melior doris delila	xanthocles melior doris delila erato demeter erato lativitta	aoede lucretius xanthocles melete doris delila erato venusta erato lativitta	aoede doris delila erato amazona	aoede bartletti doris delila erato lativitta			
III. *phyllis* pattern. F.-w. with discal red H.-w. with yellow band					amaryllis rosina	amaryllis rosina		amaryllis					nanna besckei	
				petiveranus	petiveranus hydarus columbinus	petiveranus		erato phyllis	erato phyllis				erato phyllis	
IV. *sapho* pattern. F.-w. discal yellow or white H.-w. marginal yellow or white					cydno cydno cydno temerinda cydno epicydnides	cydno chioneus cydno galanthus	cydno alithea							
					sapho eleuchia	sapho leuce	sapho primularis							
V. *himera* pattern. F.-w. discal yellow H.-w. discal red				doris eratonia clysonimus	doris eratonia clysonimus hortense	doris transiens doris eratonia clysonimus hortense	hierax himera clysonimus hortense							

The second is apparently centred round *Mechanitis lysimnia*, Fab., and includes *H. narcaea* and *H. narcaea polychrous*.

Association III is the Upper Amazon or Ega type, containing dark brown forms and including *Mechanitis egaensis*, Bates, and a form of *H. pardalinus* and seven species of other subfamilies.

Association IV is described as the Bolivia, Ecuador and Peru type, characterised by orange-tawny markings on a black ground and including *Melinaea mothone*, Hew., and *H. aristiona aristiona* also.

Ithomiinae 4
Satyrinae 2
Nymphalinae 3
Heliconinae 2
Acraeainae 1
Papilioninae 2
Hypsidae 2

M. C. Oberthür has published an interesting account,[*] with a wealth of illustration, of the variation of *H. vesta* (*erato*) and *H. thelxiope* (*melpomene*), in which he shows how the variations of one are exactly copied by the variations of the other throughout their range. He comes to the remarkable conclusion that, whilst the two species can be distinguished in nearly all their localities, they each ultimately produce a form which he calls *melpomene*, and the *melpomene* form of *vesta* is indistinguishable from the *melpomene* form of *thelxiope*. Oberthür's figures of these *melpomene* forms are equivalent to *H. erato callycopsis*, f. *viculata* and *H. melpomene melpomene* f. *atrosecta* respectively. Oberthür was, of course, unaware of the character separating the genus into two sections, though his two forms of "*melpomene*" can also be distinguished by the shape of the red band on the fore-wing.

It may be interesting to note the geographical distribution of some of the characteristic patterns of the genus, and the appended table (Table II) shows the range of five such patterns. It is based on existing information as to the localities in which the forms named have been taken. Such information is, of course, of a positive nature, whereas the absence of any record of a form from a given locality is merely negative evidence of its non-occurrence. In the case of the "*melpomene*" pattern (No. 1) forms of Section I are accompanied by forms of Section II in seven out of ten localities. Applying the same method of analysis to the first four selected patterns, we find that of twenty-four occurrences of such patterns appertaining to members of Section I, twenty-one are accompanied by corresponding patterns in members of Section II. The fifth pattern occurs only in members of Section II, and in this case no species occurs without another which resembles it, whilst in Ecuador no less than four species having this coloration form an interesting group.

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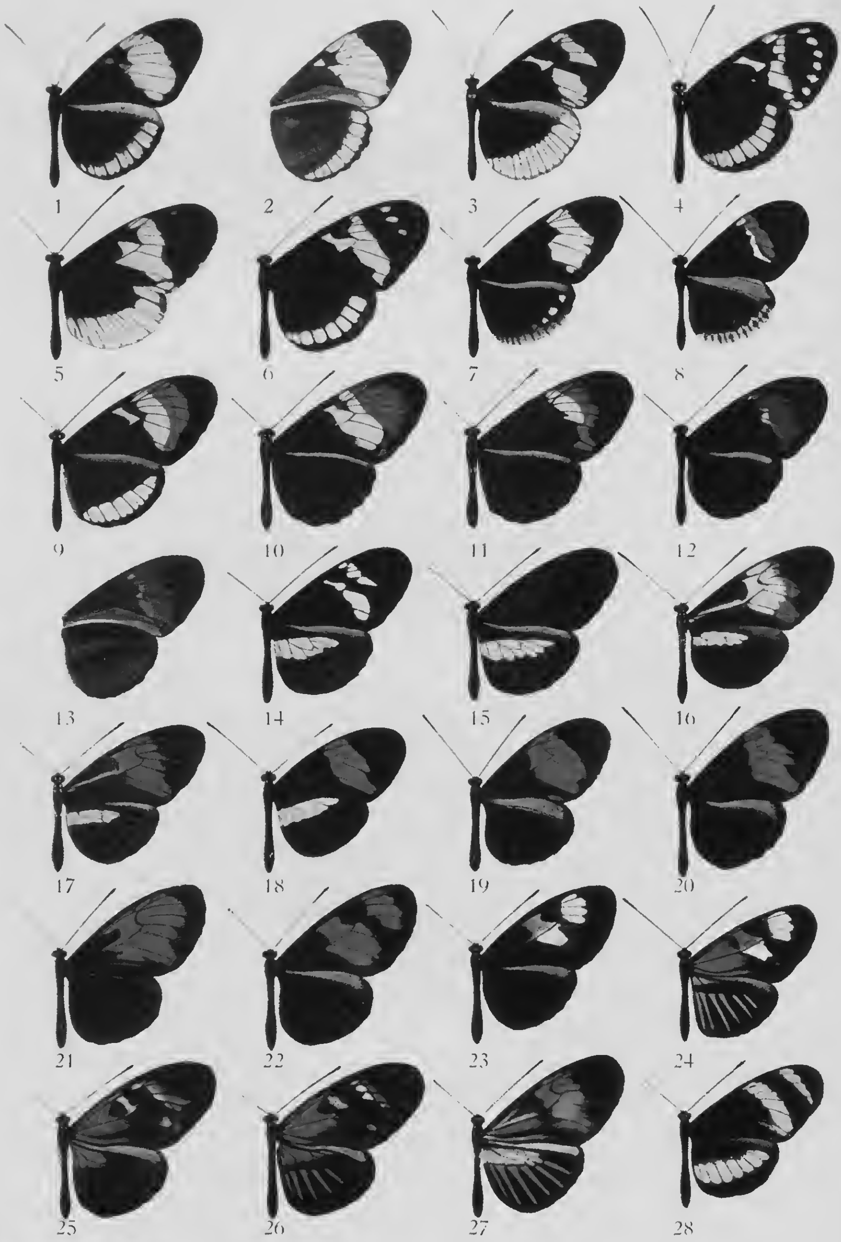
[*] Étud. d'Ent., 21, 1902.

In the light of present information there seems little more to be said with reference to these resemblances. That the genus *Heliconius* contains only some thirty good species instead of about seventy is not a very surprising conclusion in view of the methods hitherto adopted in species determination, and the fact that probably no other genus of Lepidoptera exhibits so great an instability of pattern. The remarkable varietal and mimetic phenomena exhibited by the two sections of the genus provide, however, a field of valuable research, calling for an experimenter who can carry out in S. America the class of work we inevitably associate with the names of Marshall, Sywnnerton, Lamborn, and Carpenter in Africa.

EXPLANATION OF PLATES XI–XVII.

[*See Explanations facing the* PLATES.]

Trans. Ent. Soc. Lond., 1916, Pl. XI.



[illegible] Eltringham, [illegible]

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FORMS OF HELICONIUS MELPOMENE.

Explanation of Plate XI.

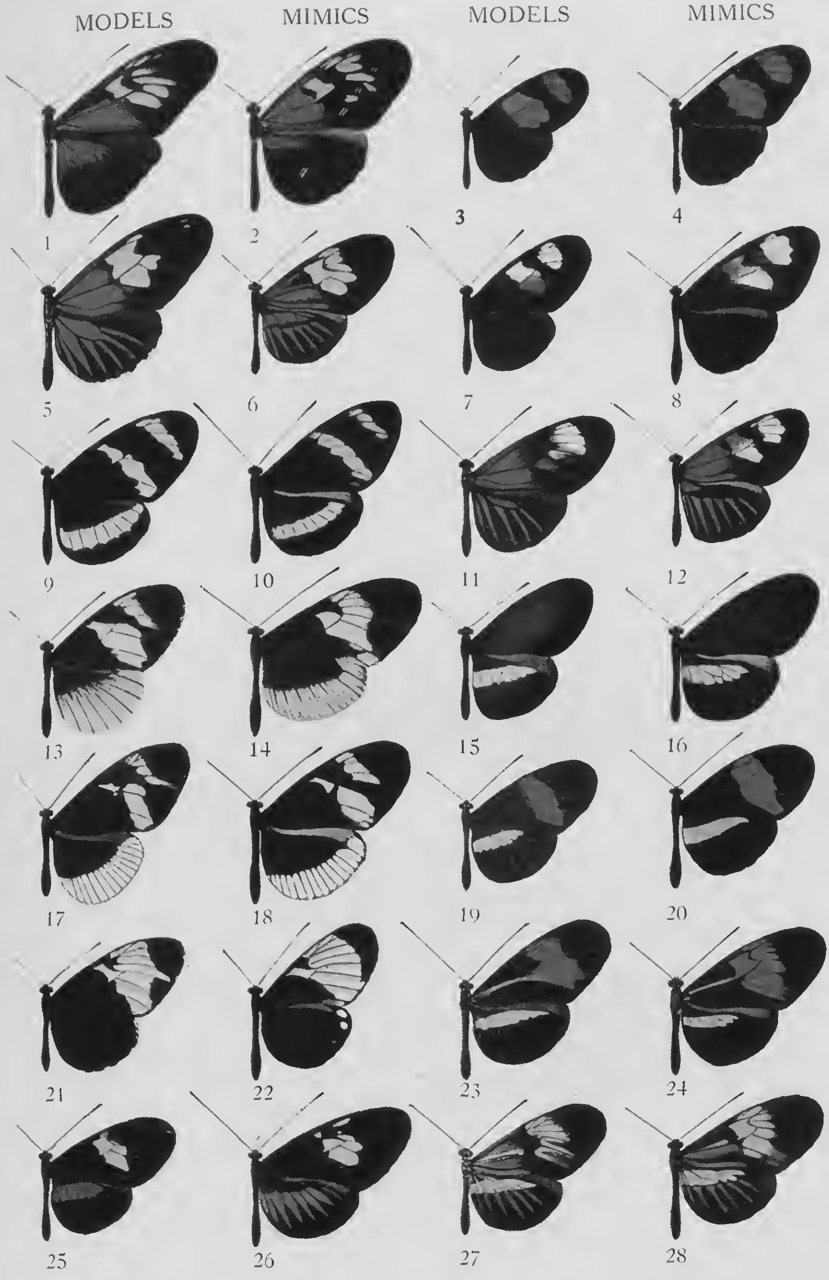
Forms of *Heliconius* apparently conspecific with *H. melpomene*.

Fig. 1. *H. cydno cydno*, Doubl.
2. ,, ,, ,, (underside).
3. ,, ,, *cydnides*, Staud.
4. ,, ,, *hermogenes*, Hew.
5. ,, ,, *alithea*, Hew.
6. ,, ,, *hahneli*, Staud.
7. ,, ,, *zelinde*, Butl. (near).
8. ,, *vulcanus cythera*, Hew.
9. ,, *heurippa wernickei*, Staud.
10. ,, ,, *heurippa*, Hew.
11. ,, ,, ,, f. nov.
12. ,, ,, *rubellius*, Gr.-Sm. (near).
13. ,, ,, ,, (underside).
14. ,, *weymeri weymeri*, Staud.
15. ,, ,, *gustavi*, Staud.
16. ,, *melpomene penelope*, ab. *pluto*, Stgr. (near).
17. ,, ,, *amandus*, Sm. and Kirb.
18. ,, *amaryllis rosina*, Boisd.
19. ,, ,, *euryades*, Riff.
20. ,, *melpomene melpomene*, Linn.
21. ,, *xenoclea confluens*, Lathy.
22. ,, ,, *xenoclea*, Hew.
23. ,, ,, *corona*, Niep.
24. ,, *melpomene isolda fibaria*, Niep.
25. ,, *melpomene funebris deinia*, Moschl. (near).
26. ,, ,, *tyche*, Bates.
27. ,, ,, *penelamanda*, Stgr.
28. ,, *pachinus*, Hew.

EXPLANATION OF PLATE XII.

INTRAGENERIC MIMICRY IN *Heliconius*.

FIG. 1. *H. egeria egerides*, Staud.
2. ,, *melpomene cybele*, Cram.
3. ,, *notabilis microclea*, Kaye.
4. ,, *xenoclea xenoclea*, Hew.
5. ,, *burneyi hübneri*, Staud.
6. ,, *melpomene penelope*, Staud.
7. ,, *notabilis notabilis*, Godm.
8. ,, *xenoclea corona*, Niep.
9. ,, *hewitsoni*, Staud.
10. ,, *pachinus*, Hew.
11. ,, *erato rothschildi*, Niep.
12. ,, *melpomene isolda fibaria*, Niep.
13. ,, *sapho primularis*, Butl.
14. ,, *cydno alithea*, Hew.
15. ,, *hydarus chestertoni*, Hew.
16. ,, *weymeri gustavi*, Staud.
17. ,, *sapho eleuchia*, Hew.
18. ,, *cydno cydnides*, Staud.
19. ,, *hydarus colombinus*, Staud.
20. ,, *amaryllis rosina*, Boisd.
21. ,, *sapho leuce*, Doubl.
22. ,, *cydno galanthus*, Bates.
23. ,, *erato phyllis*, Fab.
24. ,, *melpomene amandus*, Sm. and Kirb.
25. ,, *himera*, Hew.
26. ,, *melpomene timareta contiguus*, Weym.
27. ,, *erato anacreon ottonis*, Riff.
28. ,, *melpomene*, f. *penelope margarita*, Riff. (near).



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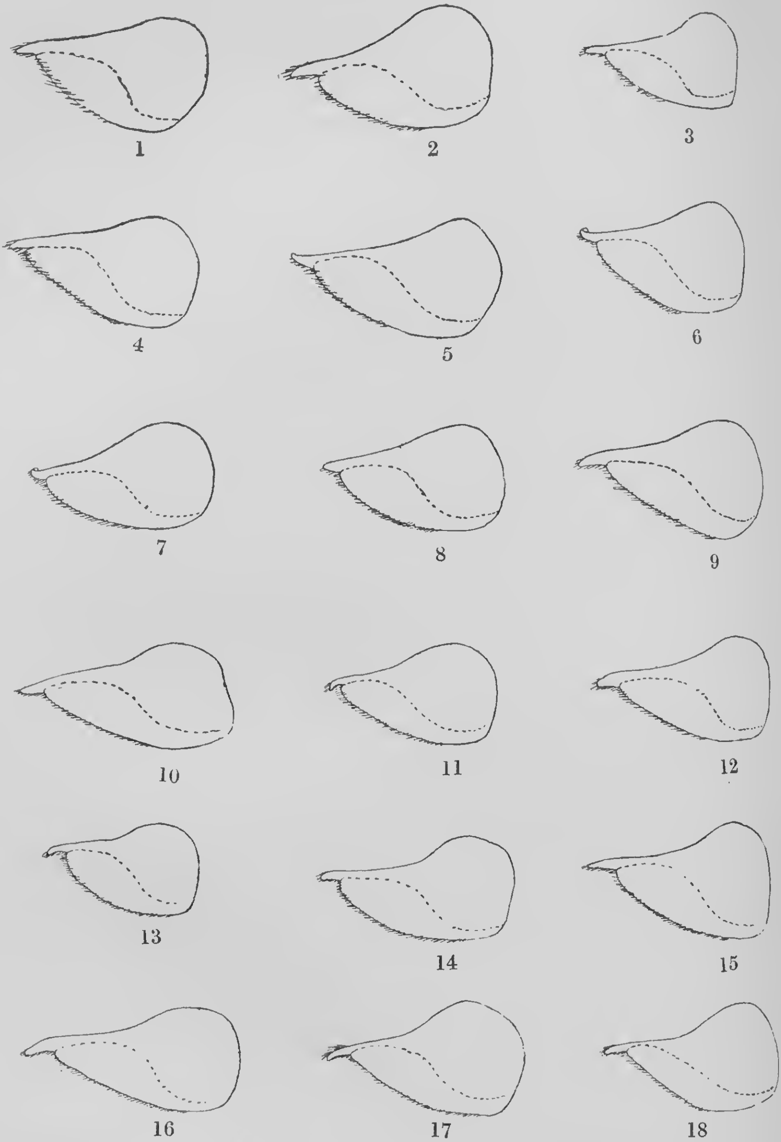
GENUS HELICONIUS, MODELS AND MIMICS.

Trans. Ent. Soc. Lond., 1916, Plate XIII.



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CLASPERS OF HELICONIUS.

Explanation of Plate XIII.

Outlines of Male Claspers in *Heliconius*.

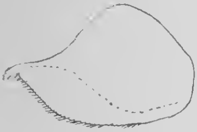
Fig. 1. *narcaea narcaea.*
2. ,, *satis.*
3. ,, *polychrous.*
4. *numatus numatus.*
5. ,, *superioris.*
6. ,, *guiensis.*
7. *silvana silvana.*
8. ,, ,,
9. *ethilla ethilla.*
10. ,, ,,
11. ,, *tyndarus.*
12. ,, ,,
13. ,, *aerotome.*
14. *gradatus thielei.*
15. *ethilla metalilis.*
16. ,, *claudia.*
17. *novatus novatus.*
18. ,, *leopardus.*

Explanation of Plate XIV.

Outlines of Male Claspers of *Heliconius*.

Fig. 1. *novatus mira.*
2. *hecale.*
3. *aristiona aristiona.*
4. ,, *tarapotensis.*
5. ,, *lenaeus.*
6. ,, *messene.*
7. ,, *aurora.*
8. ,, *arcuella.*
9. ,, *floridus.*
10. *ithaka.*
11. *pardalinus lucescens.*
12. *fortunatus spurius.*
13. *paraensis latus.*
14. *quitalenus quitalenus.*
15. ,, *felix.*
16. *anderida anderida.*
17. ,, *melicerta.*
18. ,, *holocophora.*

Trans. Ent. Soc. Lond., 1916, Plate XIV.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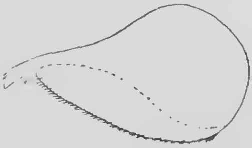
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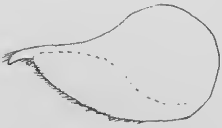
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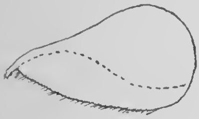
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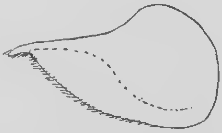
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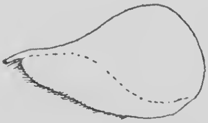
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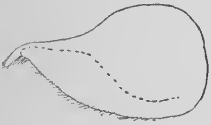
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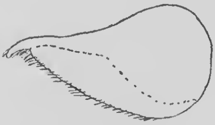
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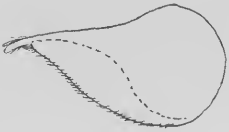
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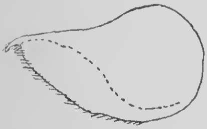
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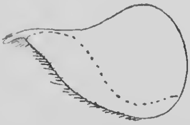
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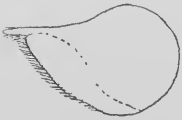
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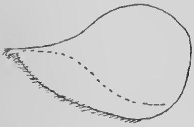
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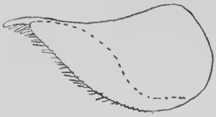
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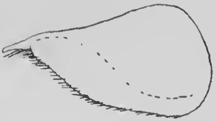
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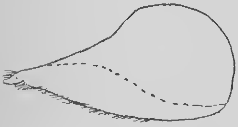
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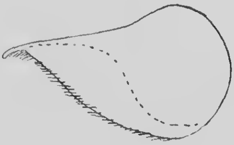
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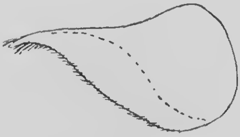
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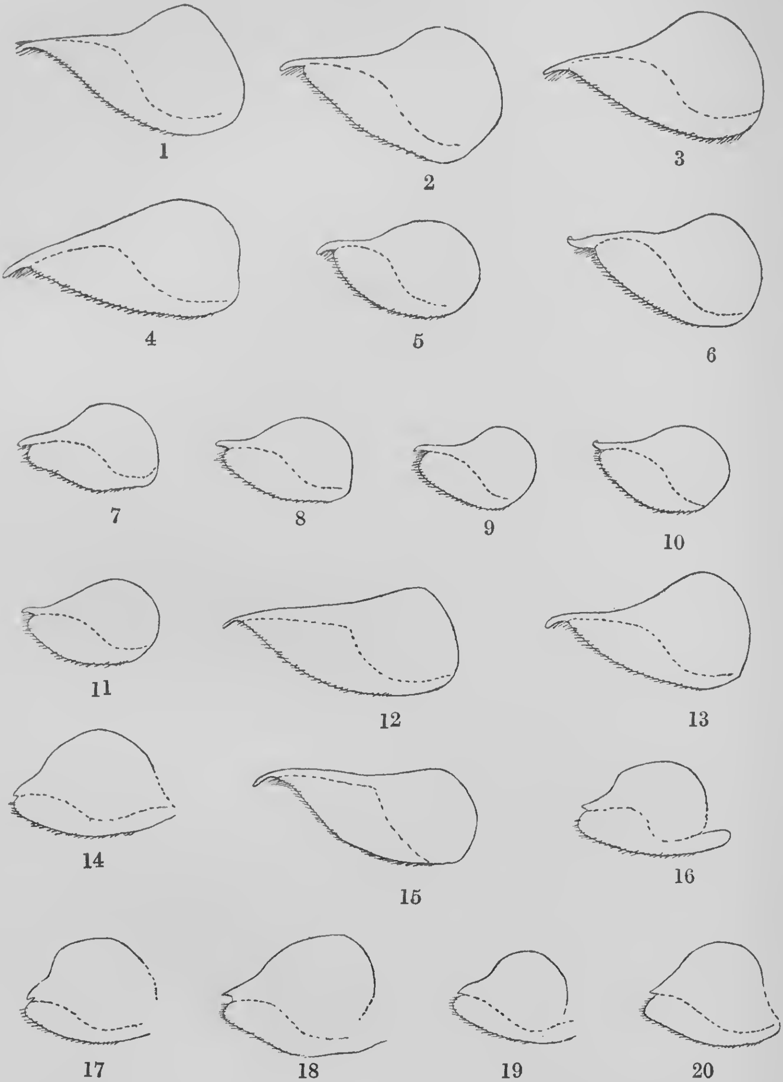
CLASPERS OF HELICONIUS.

Trans. Ent. Soc. Lond., 1916, Plate XV.



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CLASPERS OF HELICONIUS.

EXPLANATION OF PLATE XV.

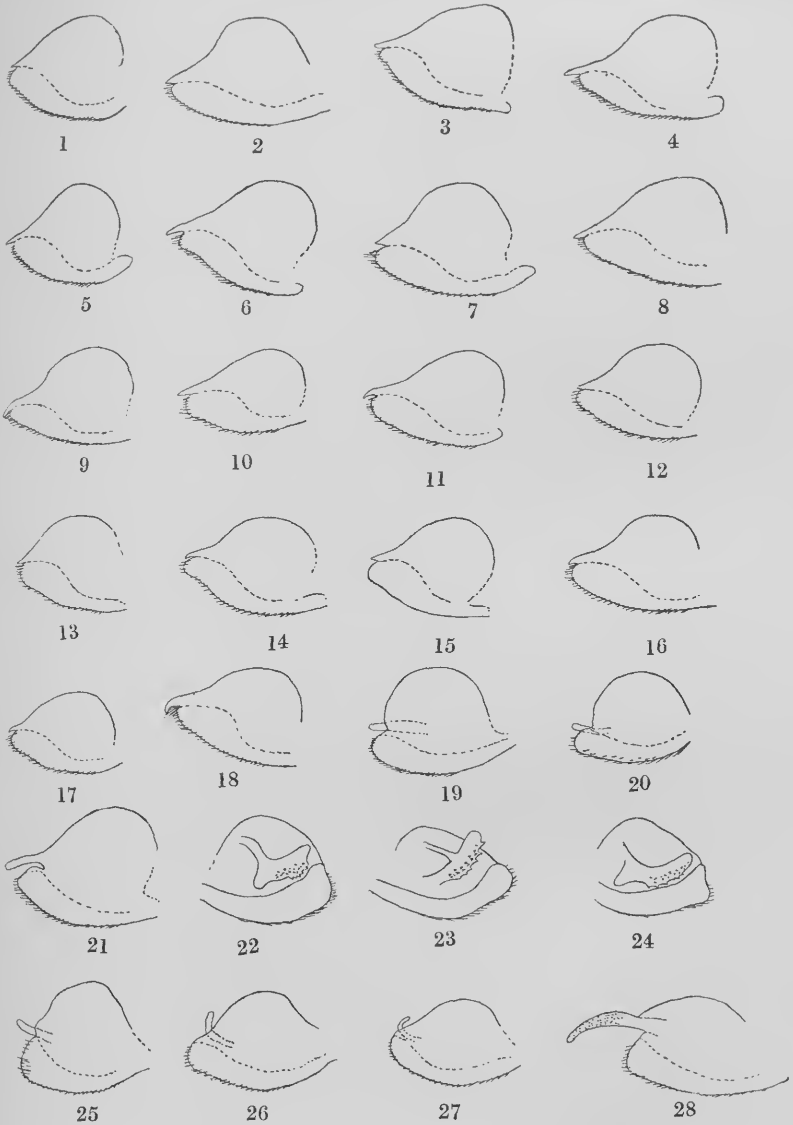
OUTLINES OF MALE CLASPERS OF *Heliconius.*

FIG. 1. *anderida albucilla.*
2. ,, *zuleika.*
3. ,, *fornarina.*
4. *aulicus.*
5. *sergestus.*
6. *vetustus metellus.*
7. *ismenius ismenius.*
8. ,, *faunus.*
9. ,, *telchinia.*
10. ,, *clarescens.*
11. "*silvana*" *metaphorus.*
12. ,, *robigus.*
13. *atthis.*
14. *cydno cydno.*
15. "*silvana*" *ethra.*
16. *cydno cydno.*
17. ,, *galanthus.*
18. ,, *zelinde.*
19. ,, *epicydnides.*
20. *weymeri gustavi.*

Explanation of Plate XVI.

Outlines of Male Claspers of *Heliconius.*

Fig. 1. *pachinus.*
2. *heurippa.*
3. *melpomene melpomene.*
4. ,, *thelxiope.*
5. ,, ,,
6. ,, *eulalia.*
7. ,, *timareta contiguus.*
8. ,, *funebris cybele.*
9. ,, *thelxiope augusta.*
10. ,, *adonis.*
11. *amaryllis euryades.*
12. ,, *rosina.*
13. *vulcanus vulcanus.*
14. ,, ,,
15. ,, *cythera.*
16. *xenoclea.*
17. *nanna.*
18. *besckei.*
19. *hecuba.*
20. *choarinus.*
21. *hecalesia.*
22. *metharme.*
23. *aoede.*
24. ,, *astydamia.*
25. *xanthocles.*
26. ,, *melior.*
27. *hierax.*
28. *egeria egerides.*



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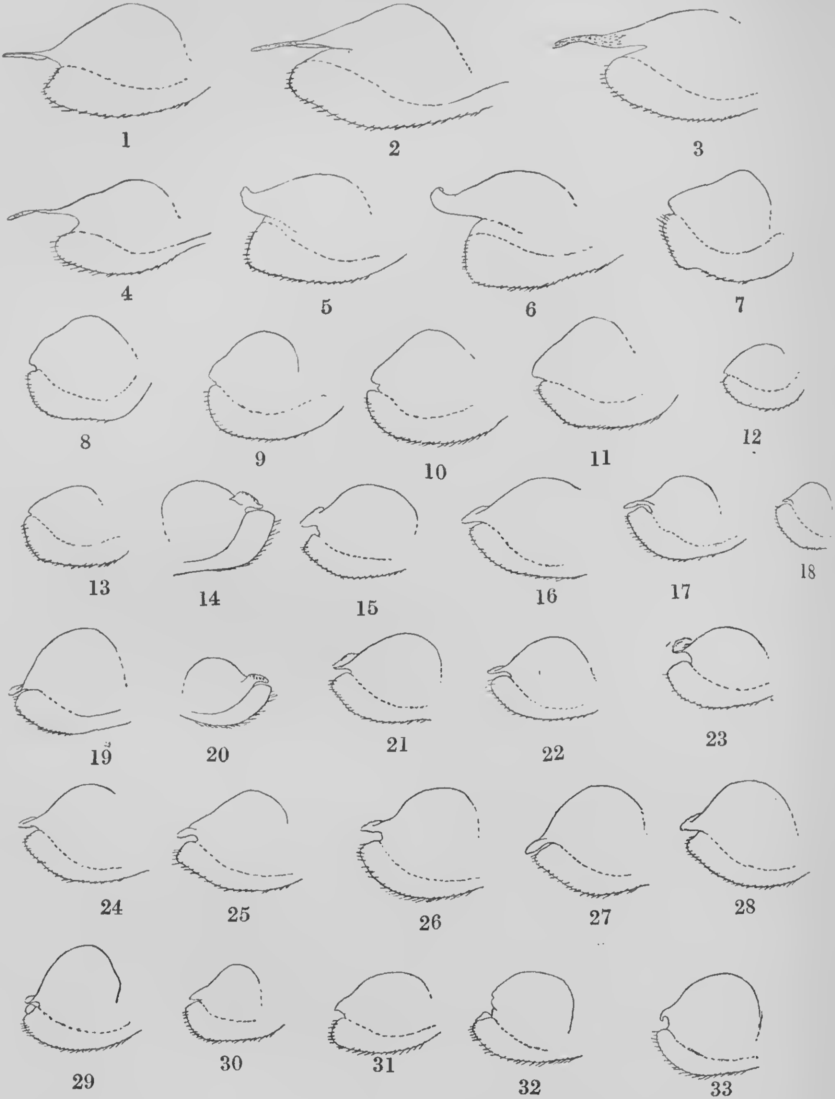
CLASPERS OF HELICONIUS.

Trans. Ent. Soc. Lond., 1916 Plate XVII.



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CLASPERS OF HELICONIUS.

EXPLANATION OF PLATE XVII.

OUTLINES OF MALE CLASPERS OF *Heliconius*.

FIG. 1. *burneyi.*
2. ,, *hübneri.*
3. ,, *catharinae.*
4. *wallacei.*
5. *doris doris.*
6. ,, *delila.*
7. *hewitsoni.*
8. *congener.*
9. *sapho eleuchia.*
10. ,, ,,
11. *antiochus alba.*
12. *leucadia.*
13. *sara.*
14. *himera.*
15. *notabilis microclea.*
16. ,, *notabilis.*
17. *cyrbia cyrbia.*
18. *petiveranus petiveranus.*
19. *favorinus.*
20. *petiveranus tristis.*
21. *hydarus hydarus.*
22. ,, *colombinus.*
23. ,, *chestertoni.*
24. *erato erato.*
25. ,, *amazona.*
26. ,, *magnificus.*
27. ,, *estrella.*
28. *amphitrite amphitrite.*
29. *hermathena.*
30. *charithonia.*
31. *telesiphe.*
32. *clysonimus.*
33. *hortense.*

V. *A reply to Dr. Eltringham's paper on the genus* Heliconius. By W. J. Kaye, F.E.S.

[Read April 5th, 1916.]

In reviewing Dr. Eltringham's groupings of the species of *Heliconius* by their genitalia, it is necessary to be very cautious as to the classificatory value of these organs. In some cases close relationship is, on account of practically identical genitalia, liable to be mistaken for co-specificness. No doubt these dissections would be helpful, and where corroborative evidence was forthcoming with series of specimens showing every gradation the results might be regarded as proved. But even in the supposed identical species *melpomene*, *heurippa*, *amaryllis*, *vulcanus*, *xenoclea*, *nanna*, which Dr. Eltringham now considered should include even such hitherto supposed well-differentiated species as *cydno*, *weymeri* and *pachinus*, there is not enough evidence at present in the form of intergraded specimens to make that conclusion wholly acceptable, especially for the last. With the others I am disposed to agree they are probably one species. *Pachinus* seems to offer the greatest difficulty, as it only occurs in Chiriqui and Costa Rica and is there accompanied with *rosina* (without doubt a local form of *melpomene*), but the two show no tendency to unite. Here there would be two subspecies of the same species occurring side by side, which is an untenable position as we at present understand species and subspecies.

Similarly *cydno* and *hermogenes* occur together at Muzo in Colombia, but do not intergrade. *Cydno* always has a white band to the hindwing. It sometimes replaces the yellow band of forewing with a white band, and is then known as *chioneus*. *Hermogenes* always has a yellow band to the hindwing. *Temerinda* is no doubt a form of *hermogenes*, with the spots of the forewing united into a band. Both of these latter forms could have either white or yellow forewing bands or spots, but never, so far as is known, a white hindwing band.

The solving of the *tumatumari* mystery is very satisfactory. *Tumatumari* occurs with *pyrforus* and other species in the Potaro district of British Guiana. When I described *pyrforus* as a subspecies of *vulcanus*, I did so feeling that it could not possibly be a subspecies of *melpomene*, as *tumatumari* appeared to be another subspecies linking on to *thelxiope*. More recently I have felt convinced that *vulcanus* and its subspecies were really forms of *melpomene*. Now Dr. Eltringham has made the discovery that *tumatumari* is a widely removed species, and thus the old difficulty of two co-existent subspecies vanishes. That *tumatumari* should show strong resemblance to the silvaniform genitalia is remarkable and almost unique among melpomeniform-looking insects. There are probably other species that are as yet undiscovered.

There is one other point in connection with all the forms proposed to be included under *melpomene*. It is somewhat anomalous if one united all the Melpomeniformes and Cydnoformes as one species that *besckei* should be left out. It occurs only above 2500 ft. in S. Brazil, and is far commoner at 3000 ft. It is possible that it replaces *nanna* of a lower elevation, but intermediates between the two are apparently unknown. Moreover, *nanna* is always rare and *besckei* very common. I feel disposed to think that Dr. Eltringham is right in separating it as distinct from *melpomene*, but this seems to rather weaken the case for all the other forms being one species, especially as *besckei* is only slightly different.

The companion species of group II, viz. *erato*, which Dr. Eltringham thinks should include *himera*, *microclea*, *cyrbia*, *favorinus*, *petiveranus*, *hydarus*, and *amphitrite*, is very possibly and even probably true to a large extent, as intergrading series of several have already been found. On the other hand, there is the same difficulty with this group as with *melpomene*. In some cases, such as *cyrbia* and *himera*, we find two constant forms occurring together. Such is the case with these two at Loja in Ecuador. *Erato* is, however, locally so extraordinarily polymorphic, such as in East Bolivia, that it is quite likely intergrades of even *himera* and *cyrbia* will be found in some locality yet to be discovered.

In the Proc. Ent. Soc., 1907, p. xiv, I had already suspected *notabilis* of being an extreme form of *erato*. There is no longer any doubt that many Heliconius species can interchange the colours red, white and yellow, and as *plesseni* can be found intergrading with *xenoclea* there is ground for supposing that the white-banded *cydno* could possibly intergrade with *heurippa*, which is half red and half yellow-banded, and even with *melpomene* itself. The extreme rarity in some cases of white-banded Heliconine forms in place of yellow-banded is a matter for future investigation. *H. telesiphe*, *clysonimus*, and *doris*, the last in both its red and blue form, very rarely occur with white bands on the forewing, yet a species like *antiochus* occurs white-banded over an immense area, and only in a few restricted areas at a considerable elevation is it yellow-banded.

It seems possible that in this case a varying intensity of light might account for the change, in just the same way as many flowers, seemingly white, under the influence of strong light develop a pink pigment. Such, for example, as some kinds of roses and tulips, which will remain white for some days before any colour appears and will even remain white if the weather be dull without sun.

The double spotting of *xenoclea*, *plesseni*, *adonides* and *nicpelti*, etc., might be looked upon as another phase of the single spot of *melpomene* breaking up in just the same way as is now known the *thelxiope* spotting is a breaking up of the single spot. In *erato* also the same transitions could easily be traced between the solid spot of *magnifica* and the intermediate semi-broken spot of *calliste*, *callycopis*, *elimaea* and *udalrica*. Forms of *plesseni*, *notabilis*, *xenoclea* and *microclea* have been recorded and figured where the spots were confluent, at once suggesting a *melpomene*-like insect.

In looking at the wonderful changes which both *melpomene* and *erato* are known can undergo, there are some interesting comparisons to be made from fresh-caught specimens and specimens of the same form that are some years old. It is to be seen that in fresh examples of such insects as *feyeri*, *udalrica*, *andremona*, etc., the red markings are all uniformly brilliant. But after about two years the red at the base of the forewing and the streaking of the hindwing becomes brown-red, while the red of the band or blotch of the forewing retains its brilliant colour for some years longer. This no doubt indicates the ancestral character of the forewing blotch and the much more recent and less staple other red marks.

In some cases an approach of one to another form may be an instance of mimetic approach. Such cases are common with the *Heliconii* such as *H. aoede astydamia*, *H. egeria egeria*, and *H. burneyi catharinae*, which all belong to group II and occur together in the Potaro district of British Guiana. The red marks on the undersides of all forms of *cydno* are sometimes reproduced on the underside of *weymeri*, but these might only be mimetic. *H. choarinus* shows this red marking beneath, but is in no way related to *cydno*, as it belongs to group II.

With the two groups of forms united respectively under *melpomene* and *erato* it is, however, just possible that Dr. Eltringham's contention of their respective co-specificness may be correct. But at present there is a great deal of proof still needed and several obstacles to be overcome.

With several of the other groupings I am afraid I could not agree. *Numata* and *silvana* are, I feel sure, always distinct, and although *numata* varies enormously it is easily separable from the much more stable *silvana*; in British Guiana they would form two subspecies occurring together. With part of the remainder of the forms which Dr. Eltringham groups together into (1), composed of *narcaea*, *ethilla*, *gradatus*, *sulphureus*, it is possible they might be the same, although *narcaea* does not come very close in fascies, but it is significant that going northwards from Rio its habitat, on arriving at Bahia the characteristic white apical patch has become yellow, while further north it is possible the yellow patch might be found broken up into a spotted band so characteristic of a number of the forms proposed to be united.

With Dr. Eltringham's group of species number (2) at the present time it seems impossible to unite *aristiona* with *ithaca* and *aulicus*. *Ithaca* in the female is no doubt a mimic of *aristiona messene*. The two sometimes occur together, but show no tendency to form one species. *Hecale*, *ithaca*, *quitalenus* and *anderida* are quite possibly the same, though the first two needed further proof. The form *fulvescens* figured in the P.Z.S., 1906, Pl. XXXIV, fig. 1, might be an aberration of *hecale* (*pasithoe*), or, as has been suggested by Mr. P. I. Lathy, it might be a hybrid between *vetustus* and *hecale*. *Vetustus* occurs along several of the rivers of British Guiana, including the Demerara, while *hecale* is seemingly confined to the latter.

Atthis (4) is found to be indistinguishable from *aristiona lenaeus*. This must be only coincidence. No one could ever suggest it was the same species. I do not think that it could ever even pair with any form of *aristiona*, being separated by the Andes. It occurs at from 1500 to possibly 3000 ft. on the Pacific slope of Ecuador, while *lenaeus* is on the eastern slopes.

Metharme Dr. Eltringham groups with *aoede*, and finds the claspers of these different from all others. This grouping together certainly looks wrong. The geographical distribution of these two is similar, but not identical. The former being more western, occurring at Ega on the Amazon, and stretching to Pebas and Iquitos into Colombia. It is never an abundant species and occurs only sparingly. The locality British Guiana often quoted must, I think, be an error. It is a very constant species, and practically no variation is found. With *aoede* very definite geographical races are found in British Guiana, the lower Amazon, the upper Amazon and Peru. The species is in some localities quite plentiful, as on the lower Amazon, especially about Para, which produces the typical form.

There is nothing beyond the genitalia to even suggest they might be the same. The body is entirely black in *metharme* except for a yellow streak below on the abdomen, while all the subspecies of *aoede* show the pairs of subdorsal yellow spots, and these show no sign of varying. Again, the apical yellow band of *metharme* is in quite a different position to any part of the group of yellow spots of *aoede*.

Then *sappho*, *antiochus*, *leucadia* and *sara* are found to be indistinguishable. *Leucadia* and *sara* might well be the same species, as some forms of *leucadia*, such as *pseudorhea*, are exceedingly like some forms of *sara*. But that *sappho* and *antiochus* could also be the same species seems improbable. *Antiochus* at low levels is exceedingly constant. At higher elevations it is very frequently yellow instead of white-banded, and at certain localities (always above 3000 ft., I believe) it is even constantly yellow-banded as in the form *aranea*. *Sara* is present frequently where *antiochus* is found, but there does not appear to be any cause to think they are the same. *Sara* is smaller, of a different shape, and is always yellow-banded from sea-level up to 3000 or 4000 ft., varying only geographically in the width of the band. *Sappho* has quite a different geographical range, and occurs in its varying geographical races from Guatemala to Colombia and Ecuador, not occurring on the east side of South

America. In shape and size it is also quite different. *Sappho*, like *antiochus* and one or two other Heliconines, occurs with white bands at sea-level and low elevations, while at higher elevation it becomes yellow-banded as in *primularis*. But this change from white to yellow is not universally true in passing from a low elevation to a higher one.

Of *burneyi* and *wallacei* Dr. Eltringham says, "Some of the forms of *burneyi* are rather variable. Those of *wallacei* exhibit a structure intermediate between the extremes of those of *burneyi*." This really amounts to the fact that it is impossible to separate these two by the genitalia. Apart from the quite different fascies these two species have different antennae. The whole of the long club on the underside is orange in the different forms of *burneyi*, but black in all the forms of *wallacei*. The antennae of *burneyi* are also longer, having 40 joints against 37 in *wallacei*. On the evidence that is to hand it is quite impossible to regard these as the same species. They frequently occur together in various localities, but never show any intermediates, and in fact have very little in common except the short red streaks on the underside of the hindwing.

H. ethra and *H. robigus* are found to be alike and of a distinctive type. These are quite likely the same. They have a similar brand on the underside of the inner margin of the forewing. *Ethra* is probably the more northern race of *robigus*. It occurs with *narcaea flavomaculata* at Bahia, while *robigus* flies with typical *narcaea* at Rio and southwards. By the additional evidence of the curious brand to that of the genitalia it looks as if it was wrong to in any way connect the two forms with *silvana*, which has no such brand.

In reviewing the classificatory results obtained by Mr. Eltringham from microscopical examination of the genitalia, it appears evident that these organs are not wholly reliable in differentiating species, and that to base a classificatory scheme on this one character alone would give results, which in the light of further evidence as to geographical range, etc., would be untrue. It would be far safer to unite only those species of which we have complete transitional series, when we could take as confirmation a wholly constant genitalia. It is very necessary to be on one's guard, with a group where so comparatively little variation is found in these organs, not to accept as one species, without further proof, forms with identical genitalia. Among the moths *Zygaena lonicerae* and *Zygaena trifolii* in all its forms have the same genitalia, so also have *Plusia iota* and *Plusia pulchrina*, yet we know these to be distinct species, the two latter having distinct larvae besides well-differentiated imagines. On the other hand, where differences occur we doubtless have evidence of specific distinctness which in some of the Heliconine instances was not even suspected.

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EXTRACT FROM THE PROCEEDINGS

OF THE

ENTOMOLOGICAL SOCIETY OF LONDON,

WEDNESDAY, MARCH 19TH, 1919.

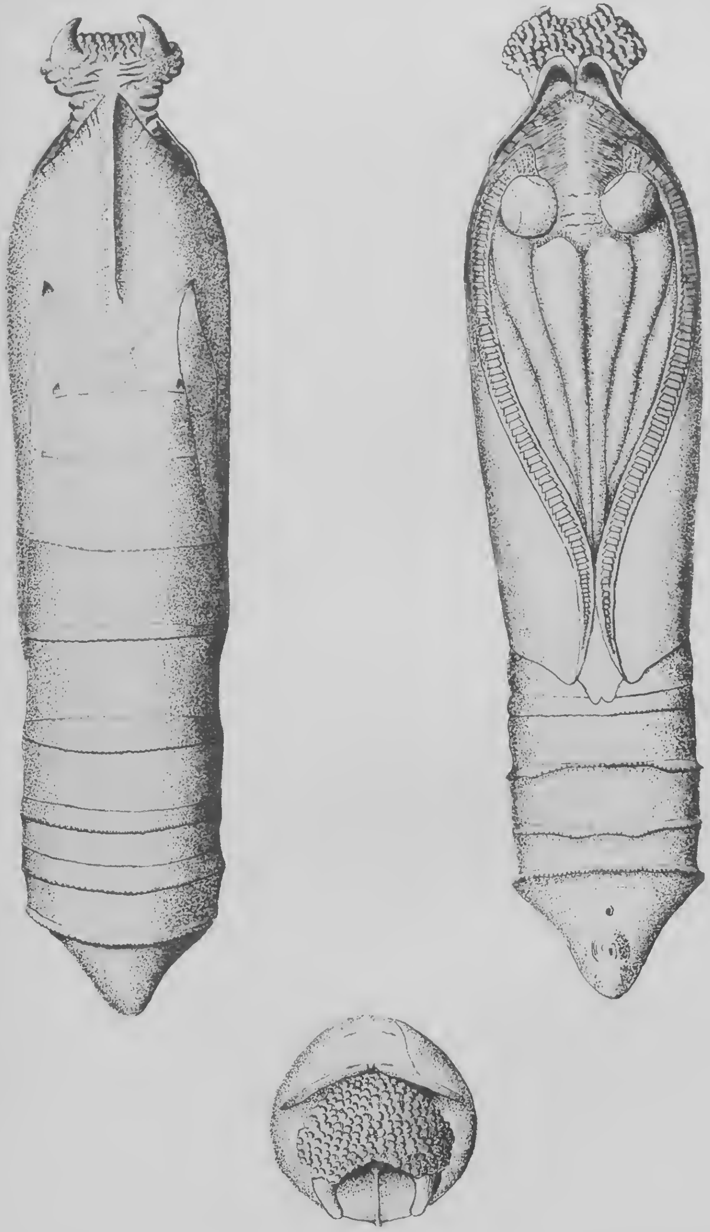
p. xiv.

NOTE ON A REMARKABLE PUPAL STRUCTURE.—Dr. H. ELTRINGHAM exhibited specimens of the pupa and imago of *Cryptophaga rubescens*, and read the following notes :—

Some time ago my friend Prof. Poulton called my attention to a remarkable pupa, which had been shown to him by Mr. J. H. Durrant, F.E.S., specimens of which are now in the British Museum (Walsingham Collection), having been collected by Mr. F. P. Dodd, F.E.S. The species is *Cryptophaga rubescens*, McLeay, of the Tineid family *Xyloryctidae*.

The larva burrows in the stems of species of Acacia, and is found at Toowong in Queensland. The female moth resembles in size and colour one of the paler varieties of our common *Tryphaena pronuba*, but without the black hind-marginal band. The male is much smaller and usually has some dark purple-brown markings on the fore-wing.

When the larva is about to pupate it takes up a position close to the entrance of its burrow, and closes the opening with a plug of silky material. These habits appear to be common to other related species, but the pupa differs from them in having a special chitinous growth on its anterior end, of such a shape as to resemble very closely the head of a wasp. p. xv. I have made drawings of the pupa which are reproduced on Plate A. It will be seen that there is at the anterior end a large more or less rounded mass of somewhat nodular structure, from which project two curved and bluntly pointed processes suggestive of mandibles. But perhaps the most curious development is that of a double ridge of chitin, the significance of which is only realised from a frontal view, when



H. Eltringham, del.

(Oxford University Press.)

PUPA OF CRYPTOPHAGA RUBESCENS, McL.

it is seen to give the appearance of two backwardly directed antennae. The extreme "waspishness" of the general effect is doubtless much enhanced when the structure is viewed in its natural position at the entrance to the burrow. It will be observed that the formation is so arranged that when the pupa is lying on its dorsal surface the wasp head is in the natural position, *i. e.* with the mandibles pointing downwards. It would be interesting to know if the pupa always lies in this position in the hole. Moreover, the roughened surface of the head gives a remarkable resemblance to compound eyes.

It may be remarked that since the burrow is plugged with silk the wasp-like mask cannot be seen in any case. This is true, but it would be of service to the pupa at the critical moment between forcing off the silk plug and the emergence of the moth. Also many pupae of this habit protrude slightly from the burrow for an appreciable period before the imago emerges, and this probably happens in the present case. It should be noted, however, that a certain wasp makes use of the deserted burrows of these and allied wood-boring larvae, whilst there is a tree cricket which preys upon the pupae, and thus the species is probably protected from the cricket by its resemblance to the wasp. The other allied species all have a roughened cap to the pupa, probably used in pushing out the silk plug, but none exhibits even an approximation to this wasp-like formation. It is one of those structures for which it seems impossible to account on any theory of mutation. It is hoped that further observations will be made, especially on the habits of the wasps which use these burrows, and the predaceous crickets. It should not be difficult to discover whether the pupae are in reality protected by their disguise.

I am grateful to my friend Mr. J. H. Durrant for assistance in making these notes.

Seasonal Dimorphism.

By Dr. F. A. Dixey, M.A., F.R.S.—*Read April 8th*, 1915.

In many parts of Europe there may be commonly seen, during the months of spring, a small brightly-coloured butterfly whose variegated mottling of tawny and black somewhat recalls the aspect of our familiar "small tortoise-shell," to which indeed it is closely related. Later on in the year the same localities are enlivened by the presence of a larger butterfly of very different appearance. This second insect shows a general ground-colour of very dark brown with an obscure mottling of a still deeper shade, the total effect being nearly black. Crossing the dark area of fore- and hindwing is a broken band of cream-colour or white; and this combination of dark ground-colour with pale median band gives the butterfly an aspect not unlike that of our British "white admiral." Of these two butterflies, the first received from Linnæus the specific name *levana*, the second was called by him *prorsa*. The generic name given to these forms by entomologists at the present day is *Araschnia*, the two insects being therefore known as *Araschnia levana* and *Araschnia prorsa* respectively.

Araschnia levana, the bright little black-and-tawny butterfly, after flying about for some time in the spring sunshine, deposits eggs, just as our small tortoise-shell does, on plants of the common stinging-nettle. From these eggs emerges a brood of spiny caterpillars, which feed upon the stinging-nettle and in due course of time turn into chrysalises. About the month of July these chrysalises disclose the perfect insect, which one would naturally expect to be like the parent butterfly. But strange to say, instead of the brightly-mottled *Araschnia levana*, what does come out of these chrysalises is the dark, pale-banded *Araschnia prorsa*. The caterpillars hatched from the eggs laid by *prorsa* feed up and pupate during the summer. Now these pupæ resulting from the eggs laid by *prorsa* may behave in either of two ways. They may either produce the perfect insect before the end of the warm weather, or they may last on as pupæ throughout the winter, not giving rise to the perfect butterfly until the succeeding spring. In the former case, the butterflies when they appear are of the *prorsa* form, like their parents; in the latter case they emerge, not as *prorsa*, but as the brightly-variegated form *levana*. We thus see that one and the same kind of butterfly may exist in two forms so different in appearance from one another that they may be, and indeed have been by good authorities, considered to belong to two entirely distinct species. This twofold aspect of the same species is what is known as dimorphism, and inasmuch as in the case that we have been considering the successive changes in aspect bear an evident relation to the successive changes of season, the particular kind of dimorphism here exhibited is known as "Seasonal Dimorphism."

The case of *Araschnia levana* and *prorsa* is perhaps the longest-known instance of seasonal dimorphism among butterflies; but it by no means stands by itself. When our attention is once drawn to the existence of this phenomenon, we can trace the presence of a similar dimorphism in many other species; though it would be difficult to find, among European butterflies at least, so well-marked a case as that which we have just had under notice. But we have not far to go before meeting with another instance of seasonal dimorphism among butterflies with which everyone in this country is familiar. The green-veined white butterfly (*Ganoris napi*), one of the smaller species of common garden white, occurs in two forms which, though very far indeed from being so diverse as *Araschnia levana* and *prorsa*, are yet quite easily distinguishable from each other. The specimens that fly in the spring have a grey tip to the forewing and the green veining of the underside strongly marked. From the eggs laid by this spring brood there results about July a brood in which the tip of the forewing is nearly black, while the green veining is much fainter and in some cases has almost disappeared. The relation of these differences with the change of season is as well-marked in this case as in the former; and although so very much slighter in degree, the dimorphism of the green-veined white is evidently similar in kind to that of *Araschnia levana*. There are many other instances among the butterflies and moths of this country where more than one brood is produced in the course of the year; and if these instances are carefully examined, it will often be found that there is a constant difference in aspect between the broods, corresponding to the period in the annual cycle to which they belong. The difference may be slight or considerable; but in no case is it so conspicuous as in the butterfly with which we began.

It is now natural to ask whether this phenomenon of seasonal dimorphism is peculiar to temperate regions such as our own country and continental Europe, or whether an analogous state of things prevails in the tropics, where seasonal conditions differ widely from our own. Only a few years ago this question would have met with an uncertain answer; now, however, we are able to make a very positive statement on the subject.

In many parts of Africa there occurs a salmon-red or brick-red butterfly with black borders and spots, known as *Precis octavia*, and in the southern and eastern parts of its range as *Precis natalensis*. This handsome insect is to be met with chiefly in the wet season. In the same parts of Africa is found, during the dry months of the year, a somewhat larger butterfly, of a dark violaceous blue colour with plentiful black markings, two conspicuous white spots near the apex of the forewings, and a deep red band running parallel with the margin of both fore- and hindwing. The name given to the insect just described is *Precis amestris*, the slightly different form found in the southern and eastern regions of Africa being known as *P. sesamus*. Looking at a specimen of *P. natalensis* side by side with one of *P. sesamus* from the same locality, we should be inclined to say that they were as different in aspect as two butterflies very well could be; and when Mr. Trimen published his famous book on South African butterflies (1887) he had no hesitation in considering them as entirely distinct from one another. But there were known at that time a few specimens which seemed to combine the characters of the two species in various proportions; one of these was figured by Mr. Trimen in his book. The existence of such transitional specimens was by him attributed to hybridisation between the two species.

It had, however, occurred to more than one naturalist that a different explanation of these intermediate forms was possible, and in the year 1896 Mr. G. A. K. Marshall made the definite suggestion that several seemingly distinct species of the genus *Precis*, including those now under discussion, could be ranked in pairs; each pair constituting a separate species existing in a two-fold form, one phase belonging to the wet and the other to the dry season. *Natalensis* and *sesamus* were thus pronounced to be seasonal phases of the same species; and two years later Mr. Marshall was able to supply an absolute proof of the truth of his suggestion, by breeding specimens of the dark blue *sesamus* from eggs laid by the salmon-coloured *natalensis*. This case is as striking in its way as that of the European *Araschnia levana* and *A. prorsa*. It was not long before Mr. Marshall obtained equally decisive proof of the correctness of his supposition in the case of another member of the same genus, for he succeeded in breeding two specimens of *Precis antilope* from eggs laid by the butterfly known as *Precis simia*. And during the next three years a similar relation was proved by breeding to exist between two more pairs of the genus *Precis*. Although the same indisputable proof has not yet been forthcoming in every other kind of *Precis*, there is now no reasonable doubt that Mr. Marshall's original suggestion was in accordance with the facts, and will in course of time be fully verified.

Many more instances of the same kind are now known to naturalists, but before considering any of these we may turn our attention for a time to the question of the meaning of these remarkable alternations in the life, not of the individual, but of the species itself. Ever since the promulgation by Darwin and Wallace of the theory of natural selection, most students of nature have trained themselves to look for some purpose in the outstanding features of all living beings. The search is not always successful, but in a very large number of cases, increasing almost every day, it is found that utility either to the individual or the species is at the bottom of the characters which come under our observation, whether of aspect, structure or behaviour. The Darwinian view of organic nature is in fact strictly teleological, a term the use of which has sometimes been considered, I venture to think undeservedly, as involving a kind of reproach. Now is there, it may be asked, any reason to suppose that the phenomenon of seasonal dimorphism is of any benefit to the species which exhibit it? It would be difficult to give an answer that would apply to all the known cases. We should have, I think, to admit that the benefit, if any, is not always obvious. We can sometimes form conjectures of a greater or less degree of probability; something may be due to the past history of the species if it could be unravelled, and still more perhaps to what is called "correlation" with a really useful feature. But there certainly are cases in which we can assign a useful purpose to the seasonal change with a very high degree of probability indeed. Such a case is to be found in the genus *Precis* that we have just been considering.

Looking at the undersides of several species of *Precis*, we can see at once that they strongly resemble dead and withered leaves. The midrib of the leaf is represented by a stripe running across both fore- and hindwing, from the tip of the former to the posterior angle of the latter. This angle is often prolonged to look like a stalk, and the surface of the wings is apt to be mottled in a manner that suggests spots of decay or growths of microscopic fungi. Examining the matter a little more closely, we find that in many cases it is only the dry-season phase of the species that puts on the dead-leaf appearance, the wet-season phase of the same species showing no such resemblance at all. (See *P. simia* and *P. antilope.*) In other species both seasonal forms are like dead leaves beneath; but when this is the case, the resemblance is greater in the dry season than it is in the wet. Now when an insect goes out of its way, so to speak, in order to look like a leaf, a stick, or a bundle of dry grass, we may conclude with very great probability that there is a meaning in this departure, and that the meaning is the necessity of concealment, either for the purpose of approaching its prey unobserved, or of itself escaping the attention of enemies who desire to prey on it. We may therefore put down these dead-leaf appearances as instances of what Professor Poulton has called cryptic coloration, that is to say, coloration whose object is concealment. But now the question arises, why should this kind of protection be so much better developed in the dry season than in the wet, and why in some cases should it not be found in the wet-season forms at all? To this question a reasonable answer can be given.

It has been pointed out by Professor Poulton that insect-eating animals of all sorts in the tropics find it much harder to get their food in the dry season than in the wet. Many insects hide themselves away altogether during the months of drought; and although several kinds of butterflies remain in evidence, they are at that time usually much scarcer in individuals than they are during the rains. The consequence of this state of things is that the struggle for life becomes much keener in the dry than in the wet season. If a species is to survive this period of stress, it has to employ some highly efficient means of protection from its enemies, who from the scarcity of their provender are very much alive to any chance of a meal that presents itself. The wonderfully close resemblance to such an object as a dead leaf affords in all probability an especially good means of protection, and no doubt many individuals of these species of butterflies owe their survival through the period of exceptional danger to this mode of defence. In the wet season, on the other hand, insect life is abundant. Many butterflies produce several successive broods in the course of the rains, and hosts of beetles, flies, and other winged creatures make their appearance at the same time. Hence the insect-eating birds and lizards find a large choice open to them of easily-obtained food; there is less occasion to search and scrutinise, and the persecution of butterflies becomes so much less strenuous, that the need for a protective disguise loses much of its urgency. Hence we find that those species of *Precis* which show so close a resemblance to dead leaves in the dry season, tend to lose part or the whole of that resemblance when the rains begin.

But although in the wet season the need for protection grows less, it does not entirely disappear. We have just recalled the fact that some species of *Precis* keep up their cryptic character during the wet months, though to a diminished extent. But we have still to account for the extraordinary change in such species as *Precis antilope* and *P. archesia*, where we have the highly cryptic dry-season phase replaced in the wet season by a form which is not only not cryptic but is actually conspicuous in a high degree. Now when we see an insect making no attempt at concealment, but flaunting, as it were, a conspicuous colour-pattern in the face of all the world, we frequently find that that insect is disliked and avoided by some of the usual insect-eating animals. Whether the avoidance is a matter of instinct, or, as is much more probable in the majority of cases, the result of unpleasant experience, it is obviously in the interest of the distasteful insect to advertise its undesirable qualities as much as possible, as for instance by brilliantly contrasted colours in conjunction with a slow mode of flight, or a choice of resting-place well open to observation. This is the well-known "warning-colour" theory of Wallace, a theory which has received much support not only from the studies of naturalists in the field, but also from experiments actually conducted upon birds and other animals in captivity. The suggestion has been made by Professor Poulton, and there is certainly a great deal to be said in its favour, that the bright colours of these wet-season forms of *Precis* are of the nature of danger-signals, warning enemies that an attack on them would be unprofitable. The likelihood of this being the true explanation is increased when we enquire into the habits as well as the colours of the species in question. Remarkable as is the change of aspect in passing from one time of year to another, the change of behaviour in the successive broods is perhaps even more astonishing. Thus in the case of *Precis antilope*, Mr. Marshall, who has had great opportunities of studying the habits of butterflies of this group in nature, informs us that "the dry-season form only frequents the bush, settling on the ground among the dead leaves, or very rarely on small plants, the underside colouring affording it excellent protection. As the season advances the habits of the insect change, and the latter form may be found . . . . frequenting open tops of kopjes, flying boldly about within a limited area, and settling with expanded wings on shrubs and bushes." With regard to *P. archesia* he notes that "the dry phase generally frequents the wooded and the wet phase the open country." The same correspondence of habit with change of aspect is also observable in the species of *Precis* from which we started, viz., *P. sesamus*. Here the underside of the dry phase, though not specially leaf-like, is well adapted for concealment in shady places. These are the places which it most affects, and, according to Mr. Marshall, "if alarmed it flies off with a rapid, and often zigzag flight, settling abruptly among rocks or herbage, when its greenish-black underside colouring is equally protective." The wet-season form, on the other hand, says Mr. Trimen, "frequents open, grassy hills, especially their summit ridges or highest points, and is very conspicuous, whether flying or settled." From all this it appears that, speaking generally, not only the aspect but also the habits of the cryptic dry-season forms are such as to aid concealment; while the behaviour of the wet-season forms seems to court observation, the choice of locality and the mode of flight being such as to display their conspicuous aspect to the best advantage. And these last are just the characters which we should look for in an insect protected by some unpalatable quality, or possibly itself palatable but depending for its safety on its resemblance to some unpalatable model. In the latter case the warning feature would of course be false instead of true, inasmuch as it would give a deceptive suggestion of a nauseous quality that did not really belong to it. This leads us straight to the interesting subject of mimicry, into which I do not propose at this time to enter, further than to remark that there is good reason to suppose that some of these wet-season forms have been affected by contact with the great group of distasteful butterflies known as Acræas, either in the way of actual mimicry, or in the way of forming with them an inedible group making use of a common warning pattern. In the latter case we should have to suppose that the dry-season phase, notwithstanding its cryptic habit, is also distasteful; for it is very unlikely, though perhaps not absolutely inconceivable, that the butterfly should accompany its seasonal change of aspect and habits with a corresponding change from nauseousness to palatability. But there is really no great difficulty here. It is true that provision for concealment generally goes with edible qualities, but there is good evidence that distasteful forms exist which adopt the cryptic mode of defence at one time, and the warning, or as Professor Poulton calls it, the aposematic mode at another. If this is true of the life of the individual, there can be no reason why it should not also obtain in the successive phases of the species, and we may therefore, I think, conclude that as regards these forms of *Precis* at least, we have gone some way towards finding the meaning of the seasonal change. In the wet season, when insect food is plentiful and enemies are fastidious, it is safe to display warning colours—whether true or false we need not now enquire—and to push them to the front. In the dry season, when food is scarce and enemies will eat almost anything they can get, the best chance is to keep out of their notice altogether. The contrast between the two forms of defence is perhaps best seen in *Precis archesia*, where, as Professor Poulton has pointed out, the very same feature, viz., the diagonal stripe from tip to posterior angle, becomes at one time a part of the cryptic sham by representing the midrib of a dead leaf, and at another time is developed into the most prominent element in a violently conspicuous pattern.

Now that we seem to have found a principle which helps us to understand the seasonal changes in these particular butterflies, let us see how far it can be made to apply to other cases of the same phenomenon. There is an interesting genus named *Byblia*, which for our present purpose may be looked upon as consisting of two species—*Byblia ilithyia*, which is common to India and Africa, and *Byblia götzius*, which is found in Africa only. Now each of these butterflies occurs in two distinct phases, so distinct from one another indeed that, just as in the case of *Precis*, they were at first thought to be different species, and received separate specific names. But from the ascertained facts of the times of their appearance, and from the very frequent occurrence of the transitional forms, much more common in these butterflies than in most species of *Precis*, it was soon suspected that the supposed distinct species were merely seasonal phases of the same butterfly. All possible doubt on the subject was set at rest by Mr. Marshall, who in each of these butterflies, *Byblia ilithyia* and *Byblia götzius*, actually bred specimens of one phase from eggs laid by a parent belonging to the other phase, thus supplying the most conclusive possible proof of specific identity. In these Byblias, it is to the underside that we must look for the chief differences between the wet and dry-season forms. In each case we find that the wet-season phase has a variegated appearance, the ground-colour being tawny and the region of the wings nearest the body being furnished with an array of small black spots. In the dry season the ground-colour of the forewings becomes darker, and the hindwing puts on an entirely different appearance. The wing is now of a deep chestnut-brown colour, and is crossed by three cream-coloured stripes. The black spots have almost disappeared; in specimens where the dry-season character is extreme, they have entirely vanished. Now comes the question, can we explain this remarkable seasonal change on the analogy of *Precis?* I think there is little doubt that we can. Looking at the underside of the dry-season form, we should at first sight be inclined to think that it must be conspicuous. But when we find from observation in the field that the butterfly is accustomed to settle with its wings closed over its back, so as to show the underside, among dried grass stems, we see that the peculiar striping is really well adapted to aid concealment. In the wet season the striping is lost altogether in *B. götzius*, partly so in *B. ilithyia.* The butterfly now presents a rough resemblance to some of the small Acraeas, and probably derives some protection from its likeness to that distasteful group of insects. That this supposition is not merely imaginary appears likely from some experiments made by Mr. Marshall with captive baboons. We have, therefore, in *Byblia* the same kind of alternation as in *Precis*, between the cryptic disguise of the dry season and the warning or mimetic aspect of the wet.

There are other cases in which the same principle will help us to an explanation. In many parts of the world the dry soil which is left exposed after the withering of vegetation is reddish in colour. It is constantly found that the undersides of butterflies belonging to certain groups assume in the dry season a reddish hue, which corresponds closely with the peculiar character of the soil. The African white butterflies with purple tips, belonging to the genus *Teracolus*, are good instances of this defensive coloration. One of these butterflies, settling on the ground and closing its wings over its back, becomes very difficult to distinguish from its surroundings, as I know from personal experience in South Africa. In the wet season a few of these butterflies retain the red-earth suffusion of their undersurface, but the greater number lose it. It is not always possible to assign any particular significance to the wet-season aspect of the insects now referred to; it may be, however, that some of them are mimics, while others may exhibit what are spoken of as "directive marks," features, that is, which serve to divert the attacks of enemies to non-vital parts, and so permit the escape of the butterfly at some sacrifice of its personal appearance. In all the cases, however, it is to be observed that the method of cryptic resemblance, which is probably the most efficacious mode of defence, is the one employed during the perilous period of the dry season. At other times of the year, when the struggle is less severe, the protection becomes correspondingly less complete. Another point to be observed is that the defensive coloration, whether cryptic or mimetic, is mainly concentrated on the under-surface, that being the surface which is exposed when the insect is at rest. This seems to indicate that the enemies against whose attacks it is most necessary to be provided, are not so much those which pursue and capture butterflies on the wing, as those that track them down and seize them when settled and at rest.

From all this it appears that we can with a good deal of probability attribute a significance founded on utility to many of these instances of seasonal dimorphism. But, as so often happens in biological enquiry, before we have gone very far we have to recognise that the case is not so simple as it looked at first sight. Let us consider another instance. The little golden-red copper butterfly, so familiar an object in our fields and gardens, has several broods in the course of the year. In a certain part of its range the butterfly is seasonally dimorphic, the spring brood being of the well-known golden-red colour, and the subsequent brood or broods, which have passed through all their stages in the late spring and summer, showing an intermixture of dark scales which give a different aspect to the perfect insect. It is impossible to maintain with any confidence that this change in appearance is of advantage to the species. We must be content with the knowledge that the dimorphism is in some way or other dependent on climatic conditions, but at this point we have to stop. We cannot, with our present knowledge at any rate, claim the seasonal variation of the copper butterfly as an adaptation to the varying conditions of its environment; the alternation between light and dark must be put down as the direct result of some external influence, probably that of temperature. The same is very likely the case with other instances of seasonal dimorphism, those for example which occur in the white butterflies belonging to the African and Asiatic genus *Belenois*.

But whether the seasonal changes are adaptive, that is to say beneficial, or not, there is no doubt that they are determined by the action of some external condition upon an organism which is so constituted as to respond to that action in a particular direction. It is not a case of simple alternation between the two phases, because we find in many instances that the number of successive broods belonging to one phase depends upon the character of the particular season to which that phase belongs. In tropical countries, for example, it is often the rule that more generations of a given species are produced during the rains than during the drought. An exceptionally prolonged wet season will give rise to an exceptionally large number of successive broods, all of the wet-season form. These wet-season broods will go on being produced until the weather changes, when they will in due course be replaced by the dry-season phase. If the species were so constituted as to produce say three wet-season generations to one dry in regular succession, the change in the butterfly would simply follow the almanack without reference to any hastening or retarding of the change of season; but, as we have seen, the generations of the butterfly tend to be regulated by the weather, however much this may happen to be out of correspondence with the usual conditions prevailing at the actual time of year.

Since then the dimorphism we are speaking of is evidently so completely dependent upon meteorological conditions, it is natural to enquire whether some of these conditions cannot be artificially reproduced, and whether we cannot by imitating the change of season, induce a butterfly which was preparing to emerge in one phase to adopt the other in its stead. A good many experiments have been made by different observers with a view to answering this question, and the results obtained by them are of great interest. An early worker in this department of research was Dorfmeister, who found that by subjecting the pupæ of the summer brood of *Araschnia levana* to a lower temperature than they would meet with under normal conditions, he was able to induce several of the resulting butterflies to emerge as an intermediate form between *levana* and *prorsa*, instead of the ordinary *prorsa*, as they would have done under natural circumstances. Several experiments of a similar kind were afterwards made by Weismann in Freiburg and by Standfuss in Zürich, but the most completely successful results with this species have been obtained by my friend Mr. Merrifield, of Brighton, a former President of the Entomological Society of London, who is certainly the greatest authority in this country on the artificial production of seasonal variations. Mr. Merrifield finds, as others have done, that by subjecting the summer pupæ of *A. levana* to a low temperature, it is possible in many instances to ensure the emergence of the butterflies as a second generation of *levana*, instead of *prorsa*. But the converse change, that of the normal winter phase into that of the summer, by applying warmth to pupæ, if possible at all, is attended with very great difficulty. On the other hand, by employing the treatment of high or low temperature in the larval (or caterpillar) instead of in the pupal period, he has succeeded in the complete conversion of either phase into the other. His experiments show conclusively that in this species it is not the pupal, but the larval stage which is most susceptible to the influence of temperature. An interesting difference between the two kinds of conversion made itself manifest in these investigations. The transformation of the summer into the winter phase was found to be readily effected in all except the very last period of larval growth, while the converse change of the winter phase into the summer was, as a rule, only brought about when the larvæ were exposed to artificial warmth from the time of hatching.

In this species, and in others experimented upon by Mr. Merrifield, there is no doubt that temperature, if not the only, is at any rate the chief determining factor in the seasonal transformation; but there is much reason to think that this is not universally the case. In tropical countries generally, the most obvious meteorological difference between the seasons is the alternation between rains and drought rather than between heat and cold; and it appears from the combined testimony of many observers, and also to some extent from actual experiment, that in such regions degrees of dryness or of moisture enter as a factor into the conditions which regulate the aspect of seasonally dimorphic butterflies. Thus Colonel Manders conducted some experiments in Ceylon which showed that abnormal conditions of dryness applied during the larval period, with no alteration of temperature, were capable of causing specimens of *Catopsilia pyranthe*, a dimorphic species somewhat resembling our "brimstone" butterfly, to assume the spring instead of the autumnal or winter aspect.

Some very interesting investigations by Mr. G. A. K. Marshall, in Mashonaland, point to a similar conclusion. There is a large genus of butterflies, mostly African, known as *Teracolus*. Many of the species of this genus are the subjects of a well-marked seasonal dimorphism; so well-marked, in fact, that for a long time the seasonal phases were treated as different species and received distinct specific names, just as in the case of *Araschnia levana* and *A. prorsa*. Mr. Marshall experimented on two of these species, *Teracolus omphale*, and *T. achine*, both white butterflies with orange tips, as follows:—He reared some larvæ which under ordinary conditions would have resulted in dry-season butterflies, under artificial conditions of warmth and moisture. The butterflies which emerged during the height of the dry season were of the wet-season phase; the transformation being a little more complete in some which had been exposed to the experimental conditions both as larvæ and as pupæ, than in others which had been so exposed as larvæ alone. On the other hand, some larvæ which had been reared under normal conditions, but subjected as pupæ to moist heat, gave rise to butterflies which showed little or no change from the dry-season forms that were captured on the wing at the same time. These experiments demonstrated that in these two *Teracoli*, as in the Araschnias investigated by Mr. Merrifield, it is the larval and not the pupal stage that is most susceptible to the climatic influence. Indeed the pupal stage in these *Teracoli* appears to be almost entirely resistant to experimental interference, while in the Araschnias it is by no means inaccessible to such influence, though much less so than the larval period.

That this principle does not hold good in all cases was clearly shown by some further experiments by Mr. Marshall on *Belenois severina*, a white butterfly common in most parts of Africa south of the Sahara. Here no perceptible effect was produced by exposing the larvæ to damp heat, but when the same artificial conditions were applied to both larva and pupa, the resulting butterflies were transformed into the full wet-season form, though the brood under ordinary circumstances would have belonged to the dry-season phase. Hence we must conclude that in *Belenois severina* it is the pupal and not the larval stage that is most susceptible. A further result of great interest emerged from the experiments on this species. When the larvæ and pupæ were exposed to moisture alone without additional heat, the butterflies were found to have assumed the bright yellow ground coloration of the hindwing underside characteristic of the wet season, while the dark veining of the same area, a feature belonging to the dry-season phase, was not only present but was strongly accentuated.

There is still another set of facts to be taken into account before we can claim to have exhausted even the elements of Seasonal Dimorphism. It is this: that even in cases where the dependence upon season of the change in aspect is well established, the two forms may often be found on the wing at the same time. Mr. Crawshay captured all three forms of *Precis sesamus*, the "wet," the "dry" and the "intermediate," within little more than a week of each other. The two forms, or phases, of *Catopsilia pomona*, were observed together in large numbers in the Kangra Valley of the Western Himalayas by Mr. G. C. Dudgeon. Other naturalists have recorded similar facts both of *Catopsilia pomona* and of its near relative *Catopsilia pyranthe*. And yet there is no doubt, on the testimony of quite first-rate authorities, that at all events in many parts of their range the diverse phases of both these butterflies are to some extent dependent on the change of season. Many other instances could be given of the simultaneous occurrence of forms well known to be seasonal, and also of forms which are closely analogous to ascertained cases of seasonal dimorphism, though the actual proof of their seasonal character may be lacking. Some of these instances of simultaneous occurrence may be put down to overlapping at the change from wet to dry and *vice versâ*, the new brood emerging while the former one is still on the wing. But there are many cases which cannot be explained in this way, and indeed all that we can safely say seems to be that several of these dimorphic phases, though under certain circumstances and in certain parts of their geographical range, they may be confined to their respective seasons, under other circumstances and in other localities may occur indiscriminately and without reference to the meteorological conditions prevailing at the time of their appearance. Taking the fact of these irregularities into consideration, we find it by no means easy to decide between two opposite views of the origin of seasonal dimorphism. On the one hand the dimorphism may be supposed to have arisen as a direct adaptation to external conditions, and afterwards, in consequence of extension of the range of the species, or of alteration in those external conditions, to have more or less fallen out of correspondence with the changes of season. On the other hand the dimorphism may have had an entirely independent origin, but have subsequently been brought, under the influence of natural selection, into a more or less intimate relation with local and seasonal conditions. It is quite conceivable that both principles may have been concerned in the production of the state of things now open to our observation.

Two further facts may be borne in mind in considering the simultaneous occurrence of different seasonal forms. One is that the members of the same brood may show great individual differences in their response to what are to all appearance identical conditions. Thus Mr. Marshall on one occasion reared under precisely similar conditions the larvæ resulting from two eggs laid on the same day by the same parent butterfly. One of these emerged as *Precis natalensis* and the other as *Precis sesamus*. The second fact is that, as we have seen, there is much difference between one species and another in the period of immature life at which the application of the requisite stimulus is most effective. In some cases, as has been conclusively shown by Mr. Merrifield, the application of artificial warmth during even the last few days of the pupal period may exert a considerable effect upon the seasonal colouring. Now it has been observed by more than one naturalist that it is in generally hot and dry localities, such as Aden, that the various seasonal forms are most often to be seen on the wing together. Such regions are liable to occasional heavy rainfalls of a temporary character, and it is perhaps possible that these sudden interruptions of the general conditions of aridity may last long enough to cause those species that happen to be in the specially susceptible stage to assume the wet-season appearance, though their actual emergence in the perfect condition may take place during the usual drought. Other species, not in the sensitive period of their life-history, may be unaffected by the temporary moisture, and may show on emergence nothing but the aspect which is ordinarily associated with the dry season. These considerations are doubtless not sufficient to account for all the apparent anomalies that occur, but they go some way towards suggesting an explanation that may apply to many of them.

We may now put together what we have learned on the subject of Seasonal Dimorphism in Butterflies.

(1) We have seen that one and the same kind of butterfly may appear under aspects so diverse that they have been considered to belong to entirely different species.

(2) These different phases of the same insect are often found to appear each at its own time of the year. Thus, in the case of *Araschnia levana*, the *levana* form appears in the spring, the *prorsa* form in the summer.

(3) Many species of butterfly which produce more than one generation in the course of the year show this kind of seasonal dimorphism. The degree in which the difference is manifested varies greatly from species to species, every transition being found between a difference so slight as to be scarcely noticeable, and a diversity so extreme that nothing short of the breeding of one form from the other could be accepted as sufficient evidence of their specific identity.

(4) Seasonal dimorphism is found not only in the butterflies of temperate regions, where the most obvious difference between the seasons is one of temperature, but also in those of the tropics, where

the change of season is principally marked by the alternation of rains and drought.

(5) In many cases, though with our present knowledge not in all, it is possible to discern utility to the life of the species in the seasonal changes undergone by successive generations. As a general rule in tropical butterflies, the dry-season phase tends to be cryptic, or adapted for concealment, and the wet-season phase to be aposematic, or adapted for the display of warning colours, which may be either true or false. The latter come under the head of Batesian mimicry. The habits of the insect may undergo a change corresponding with the difference in aspect.

(6) The method of concealment is probably on the whole a more efficient mode of defence than the method of display; and accordingly we find it more often employed in the dry season, when, from the scarcity of insect food, the need of protection against insect-eating enemies is felt in greatest measure.

(7) Seasonal Dimorphism is not a case of simple alternation of generations, but it is determined by the influence of some external condition upon an organism so constituted as to react to that influence in a definite direction.

(8) These external conditions can be imitated by artificial means. In the case of the insects of temperate countries, such as the Araschnias, the needful stimulus appears to be that of temperature; in the case of tropical insects, moisture and dryness appear to be contributing factors.

(9) The stimulus is not equally operative at all stages of growth. In some instances, as the *Teracoli*, the larval period is the most susceptible ; in others, as *Belenois severina*, the pupal.

(10) Though the dependence upon season of these changes in aspect is in many cases well established, it is often the case, especially in dry and arid districts such as the neighbourhood of Aden, that the different phases may be found on the wing together. Some of these cases may arise from individual differences of susceptibility between members of the same brood, others from a natural overlapping at the change of seasons, and others again from the effect of a temporary change in meteorological conditions upon insects that happen to be at that particular time in the most susceptible stage of their growth.

This concludes what I have to say on the present occasion about the subject of Seasonal Dimorphism in Butterflies.

XVIII. *On the Urticating Properties of* Porthesia similis, *Fuess.* By HARRY ELTRINGHAM, M.A., D.Sc., F.Z.S.

[Read October 1st, 1913.]

PLATE XXII.

IN a former note * I pointed out that the urticating properties of the female of *P. similis* were due to the presence in the anal tuft, of barbed spicules, apparently identical in structure with those of the larva, and although it seemed probable that the moth derived its spicules from the cocoon, the manner in which it did so was not very obvious, since although there are many spicules in the cocoon the body of the moth would seem to be protected from contact, even during emergence, by the pupal skin.

During the past summer I have had an opportunity of studying the subject more fully, with extremely interesting results. I am indebted to Prof. Poulton for many useful suggestions, and to Commander Walker and Mr. A. H. Hamm for a portion of the material for my experiments.

The larva, though well known, seems not to have been examined very minutely, and it may be of interest to describe the structure in relation to the spicules, as revealed by a series of sections.

The spicules occur on every segment except the first and second. The third and fourth segments have two extra large masses which meet dorsally. On each remaining segment they occur on two dorsal and two dorso-lateral projections. Plate XXII, fig. 2, shows a diagrammatic section of half a segment, the spicule tufts being marked *S*.

The large hairs (*h*) arise from chitinous sockets which seem to occur all over the larva, though especially numerous on the lateral projections. These hairs are branched as shown in the figure. Amongst the dorso-lateral spicules are found white plume-like structures, one of which is shown at Plate XXII, fig. 2 (*p*). Occasionally these arise on the dorsal tufts also. To the unaided eye their matted branches have the appearance of white spots on the larva. Fig. 1 is a diagrammatic view of a section of the larval skin including one of these plumules. From this it is seen that the spicules *S*, are borne in tufts on small chitinous papillae, each of the latter being in direct communication with a double layer of special cells *E*. The spicules themselves are finely pointed barbed structures, the thicker outer end being triradiate. They are very easily detached; in fact, it is almost impossible to touch the larva without displacing them in considerable numbers. The plume-like structure * arises from a chitinous socket, differing little, if at all, from the sockets of the larger branched hairs, and having at its base several cells *G* apparently of a glandular nature. The plume is quite as easily detached as the spicules.

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* Proc. Ent. Soc. Lond., p. lxxx, 1912.

As in so many similar cases, it is much easier to determine the morphology than the physiology of these structures. The two layers of hypodermal cells *E* doubtless secrete the spicules themselves, but whether the gland *G* does more than merely secrete the plume, I am at present unable to decide. Neither the plumes nor the spicules have any appreciable action on litmus paper. During life the plume may serve to hold spicules, or even by itself becoming detached, to carry them to a distance. At least it seems improbable that so complicated a structure should have been evolved, merely as a factor in the rather conspicuous pattern of the larva.

The large branched hairs which occur all over the larva certainly serve to hold loose spicules, although this may be only a part of their function, and they are probably also mechanically protective.

The question whether the urticating properties of these and similar larvae are due to chemical or mechanical action or to both combined, still remains unsolved. Whilst I favour the purely mechanical theory I admit the difficulty of accounting for the marked difference of individual susceptibility to the urticating spicules of different species of larvae. In my own case the spicules of *Cnethocampa pityocampa* applied in small doses produce less irritation than those of *P. similis*, and yet the former species is generally regarded as the most "venomous" of all the

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* This structure is proportionately a good deal longer than shown in the diagram.

European forms. Nor is there a great difference in the structure of the spicules, those of *C. pityocampa* being merely devoid of the triradiate barb at the thicker end.

The spicules of *C. pityocampa* have been variously said to contain formic acid, cantharidin, and no poison at all. Deegener, in the "Handbuch der Entomologie," seems to favour the theory of a combined chemical and mechanical action. I have found that the irritating effect of the spicules of this species is in no degree impaired by prolonged immersion in various solvents such as ether, alcohol, and xylol. On the sixth and seventh abdominal segments of the larva of *P. similis* there are two eversible glands which have been supposed to secrete a fluid which poisons the spicules. Of this there is no satisfactory evidence. The glands have probably a repugnatorial function. They have been described by Poulton (Trans. Ent. Soc. 1887, p. 300). The drop of moisture which often appears on these structures has no action on either red or blue litmus paper, nor indeed have I been able to detect any peculiar odour associated with them, though others seem to have noticed something of the kind.

To turn now to the imago. When full fed the larva spins a thin but tough cocoon, compounded of silk with which its own large hairs are interwoven. The inner lining of the cocoon is of much looser silk, and though spicules are scattered all through it there is a particularly dense mass of these arranged roughly in a belt round the inside of the lining, and placed towards the anterior end, a little beyond the middle, Fig. 3, *S*. The spicules adhere together in small masses probably owing to their barbed structure. By taking pupae out of their cocoons I was easily able to show that the moth obtains its spicules from the cocoon, since an imago hatched from a naked pupa never has any of these bodies in its anal tuft. I then carefully watched the emergence of imagines from naked pupae in order to see if there could be observed any appropriate movements which would result in the collection of the spicules. A male on emerging immediately crawled to the side of the box and assumed a position suitable for the expansion of its wings. The behaviour of a female was, however, quite different. Once out of the pupal skin it began a series of curious contortions of the abdomen. The latter was moved so that the anal tuft described a succession of circles, whilst by longitudinal expansion and contraction of the segments the tuft was made to open and close, the action somewhat resembling the manner in which an elephant picks up small objects with its trunk. Not every female emerging from a naked pupa made these movements, or at least not for any appreciable length of time, a fact which suggested a further experiment which I shall describe later. I now wished to see the process actually carried on in the cocoon. Since it was not possible to decide when a moth was about to emerge from a pupa when the latter was enclosed, pupae were removed by cutting off the posterior end of the cocoon. With a little practice it is possible to determine with some accuracy by the appearance of the pupa when a moth is ready to emerge. As soon as it had cracked the pupal skin it was slipped back into the cocoon the open end of which was pinned down. From a male pupa so treated the moth emerged very rapidly. The anterior end of the cocoon seems to be comparatively thin, and a thrusting movement of the head and thorax soon tore a hole through which the moth emerged and ran to the side of the box. A female treated in the same manner at first emerged only so far as the anterior part of the thorax. In this position the extremity of her abdomen was just on a level with the band of spicules in the cocoon and she proceeded to carry out the peculiar movements I have already described. The anal tuft could be distinctly seen moving round and round the cocoon and opening and shutting amongst the spicules.

It is of great interest to note that the hairs of which the female tuft is composed are specially adapted to hold these spicules when collected, since towards their proximal ends they are irregularly spinose. Fig. 4 shows the ends of a few of these hairs with one or two spicules adhering thereto.

I have already said that not every female emerging from a naked pupa made the appropriate sweeping movements, a fact which suggested that normally the stimulus of contact with the cocoon was necessary. I therefore placed such a female after complete emergence but before the wings had begun to expand, in a cocoon. Almost immediately she began to make her way out and having partially emerged proceeded to sweep up the spicules in the manner already described.

One further point remains to be elucidated. Prof.

Poulton made the ingenious suggestion that possibly the arrangement of spicules in a ring or band might be peculiar to the cocoons spun by a female larva. Unfortunately by this time I had but few cocoons left and further supplies were unobtainable. The few remaining examples were cut open and the pupae carefully sexed. Of six cocoons two contained female pupae and four male. In the former the spicules were certainly arranged in a more definite band than in the latter. In two of the male cocoons they were much less numerous, and in the remaining two were more scattered. It will be interesting to complete this observation when further material becomes available. Meanwhile we have evidence of a very remarkable instinct in the female moth, which by collecting its own larval spicules, materially adds to the protective qualities of the tuft of hair with which it ultimately covers its eggs. The spinose structure of its own hairs causes the majority of the spicules to be retained in that part of the tuft, which when eventually transferred to the eggs, lies uppermost.

The moth itself is probably distasteful, and nearly every collector must have observed the manner in which the conspicuous gold "tail" is suddenly protruded between the wings when the insect in its resting position has been disturbed. This warning action may also be associated with the presence of the urticating spicules in the tuft, the males in such case being, as males are said to be, mere deceivers.

EXPLANATION OF PLATE XXII.

(*See explanation facing the* PLATE.)

EXPLANATION OF PLATE XXII.

Porthesia similis.

FIG. 1. Portion of larval skin shown in transverse section.

C. Chitinous cuticle.

S. Tufts of urticating spicules arising from cuticular papillae.

E. Hypodermal cells associated with urticating spicules.

P. White plume-like body.

Sc. Socket of same.

G. Gland at base of plume.

2. Diagram of transverse section of larva (one half only).

h. Large branched hairs or setae.

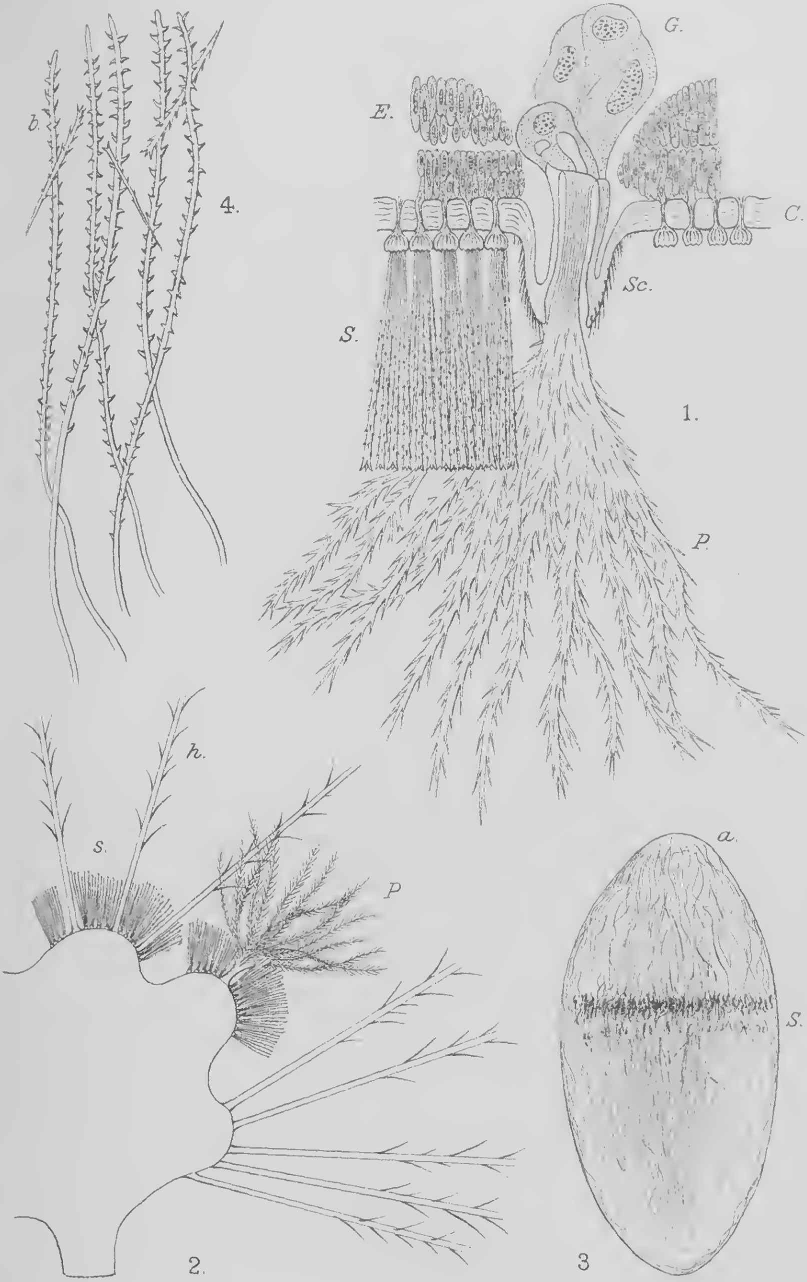
S. Urticating spicules.

P. Plume-like body.

3. Section of cocoon showing the band of urticating spicules (*S*) therein.

4. Some of the hairs (modified scales) which form the "gold tail" in the ♀ moth. Their basal or proximal ends (*b*) are irregularly spinose and so hold the urticating spicules swept by the moth from the cocoon.

(The corresponding structures in the ♂ are smooth throughout their length.)



H. Eltringham del. West, Newman lith.

PORTHESIA SIMILIS: URTICATING SPICULES &c.

TRANSACTIONS
OF THE
ENTOMOLOGICAL SOCIETY
OF
LONDON
FOR THE YEAR 1919.

I. *Butterfly Vision.* By H. ELTRINGHAM, M.A., D.Sc., F.Z.S.

[Read December 4th, 1918.]

PLATES I–V.

So much has already been written on the structure and function of the compound or facetted eye of Arthropods, that the worker who is unequipped with a profound knowledge of optics, mathematics and other sciences, may well feel some hesitancy in adding to the already voluminous literature of the subject. Nevertheless, since most works on insects in general give but a very imperfect summary of existing knowledge, whilst comparatively few papers on the insect eye are written in English, it is hoped that the observations here recorded will not be regarded as altogether superfluous.

If my examination of the matter appears to have resulted in but little that is new, at least I can claim to have repeated many of the known experiments and thus helped to remove at least some of the uncertainty which has hitherto tended to make the subject of insect vision an unstable compound of opposing theories. My attention was first called to the subject by the articles on the sense of sight written by Hess, in the "Handbuch der vergleichender Physiologie," in which he describes very extensive and elaborate experiments on animal vision. As the result of these he announces that all insects, or at least those on which he experimented, are totally colour-blind.

How many of us have not been first attracted to the study of insects by their beautiful colours and their association with flowers? So far as butterflies are concerned, colour would seem to be inseparably associated with their very existence, and to be told, with an alleged weight of evidence, that their own colours and those of their surroundings have for them no existence, is to receive a rude shock to our most cherished traditions, however clearly we may realise the obvious fact that the existence of colours is no proof that they were intended to be seen.

My original intention then was to try to carry out a series of experiments on the question of colour vision only, but closer acquaintance with existing works on insect vision convinced me that there was scope for a somewhat wider examination of the subject, in spite of the fact that, given the power of sight, by whatever means this power may be exercised, the histological structure of the creature's eyes is but little likely to demonstrate or disprove the power to distinguish colours.

The present paper resolves itself, therefore, into two parts, the nature and position of the image in the eye, together with the character of the supposed organs of perception, and secondly, the evidence for and against a capacity for distinguishing those differences in the wave-lengths of light which we ourselves speak of as colours.

Rather for the latter purpose than the former I have chosen as a type the insects referred to in the title, since the question, Do insects distinguish colours? is about as vague as an inquiry as to whether birds are black. There are many species of insects which can have no use whatever for a sense of colour, apart from the many which we know to be blind. Nevertheless, in examining the subject of insect sight we shall have to refer to insects of other orders and even to animals which are not insects at all.

THE STRUCTURE AND FUNCTION OF FACETTED EYES.

So far as the histological structure of the compound eye is concerned, the difficulties, though considerable, are not so great as those which appertain to the nature of their function. The extent of our knowledge of the vision of any creature will always have certain limits, though in the case of the vertebrate eye we feel able to attain to more nearly final conclusions, owing to our personal knowledge of our own visual powers and the known homology of other vertebrate eyes. Thus we know that in our own eyes there is a lens which can, and in fact does, project an image of external objects on to a sensitive layer, the retina, in the same way as the lens of a photographic camera throws an image on to the sensitive plate at the back. There are minor differences, such as the curved surface of the retina, the method of focal adjustment, etc., but the general principle is the same. The image is sharp and complete, and as in the camera it is upside down. That we are unconscious of the latter fact is merely due to interpretation based on experience. Objects viewed in a flat mirror appear to us to be laterally reversed though not inverted. Such operations as we habitually perform with the aid of a mirror are done with perfect facility and proper co-ordination of movement, whilst those which are not generally done by reflection, such as writing or drawing, are found, when attempted, to be extremely difficult. Nor are we normally conscious of the fact that owing to the possession of two eyes we see two images, those of near objects differing considerably, whilst those of more distant ones are less diverse. Our perceptive faculties combine the two images into one, at the same time utilising their differences to obtain an estimate of distance. The well-known stereoscopic photograph is adapted to this faculty and gives an apparently solid picture from two rather different flat ones. Examination of other vertebrate eyes shows their structure to be so similar that we are justified in assuming that their action is the same, though there are a few exceptions, such as the chamaeleon, whose eyes can be moved quite independently, and cannot be supposed to give a stereoscopic image except when they both happen to be looking in the same direction.* Also most fishes' eyes would seem to be so placed that both can hardly see the same object at once.

So far, then, we may claim to know something of the nature of our own eyes and of those which are similarly formed. The knowledge does not carry us very far. An image optically described as a real image, as opposed to what is known as a virtual image, seen in certain lens combinations, is projected on to a highly complicated nervous tissue, the retina. How that image in all its intricacy of form and colour is conveyed to and perceived by the brain, we do not know.

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* As Prof. Poulton reminds me, the chamaeleon's eyes are always co-ordinated at the moment of striking.

In the Invertebrata we find many types of eyes, *i. e.* organs whose function is to perceive light. In lower forms such organs are of so simple a character as to preclude the possibility of their doing more than detecting the difference between light and darkness. All stages of complication and multiplication are found. Some molluscs have hundreds of such organs, many of them capable of producing images, though in many cases the existence of a nervous mechanism capable of perceiving such images seems doubtful, and the value of so many eyes to creatures of such sedentary habit is rather obscure.

In other invertebrate creatures, and notably in spiders and insects, we find what are known as simple eyes or ocelli each having a single lens producing an inverted image, though to what extent such image is perceived by the animal's consciousness it is difficult clearly to define.

The most remarkable form of invertebrate eye is, however, the compound or facetted eye of insects and Crustacea.

Before summarising the various views and theories which have been advanced on the subject of the vision of the compound eye, it will be well to give some description of its structure, so that the references of former workers to its various parts may be more easily understood.

Plate I shows a section through the eye of an ordinary Small Tortoise-shell butterfly (*Vanessa urticae*) which may conveniently be taken as a type. The outer part of the eye presents the surface of rather more than a quarter of a sphere, and faces in all directions except inwards and backwards. It is separated from the corresponding eye of the other side by a hard chitinous framework, very narrow above and in front, but wider beneath, where a somewhat larger space is required for the palpi and the proboscis. The external layer of the eye is of fairly hard chitin divided into a great number of hexagonal elements, the facets, in *V. urticae* about 5000–6000 on each side. A facet consists of a minute lens, generally if not invariably colourless in the centre, but often yellow or brownish round the edges. This layer is called the corneal layer. In *V. urticae* and many other butterflies there are hairs projecting from sockets between the facets. As these are all radially arranged they do not interfere with the vision any more than do the eyelashes of vertebrates. In transverse section the lenses are more or less biconvex, and frequently, especially in butterflies, there lies beneath the lenses a layer of transparent material which has been called the *processus corneae.* Beneath this layer and corresponding to the number and position of the corneal facets are found the structures known as "ommatidia." The form of the ommatidium varies within rather wide limits. In *V. urticae* it is as follows—

Adjacent to the inner surface of the *processus corneae* is a highly refractive body of a chitinous nature and having a conical shape. It is known as the crystalline cone, or shortly, the cone. In life it is entirely transparent and apparently structureless, though in prepared microscopic specimens it is seen to consist of four cells whose contact surfaces lie parallel to the long axis of the cone. At the outer end or base of each cell is a nucleus, the so-called Semper's nucleus. The whole conical body appears in stained preparations as a cone enclosed in a sheath like a nut in its shell, and in differential staining the sheath, and sometimes the nuclei, take that stain which indicates a lesser degree of chitinisation, the cone itself usually taking the same stain as the corneal facets. At the inner or apical end the cone sheath is continued as a long transparent rod, forming the central part of the ommatidium. This rod is known as the "rhabdom" (Pl. II, fig. 2, *r.*). Surrounding it but not, in *V. urticae*, reaching quite to the cone apex, there are several (eight in *V. urticae*) elongated cells known as the retinulae, or visual cells (Pl. II, fig. 1, *ret.*). These extend backwards from near the cone apices to a transverse septum in the depth of the eye, called the "basal membrane." In butterflies, or at least in those I have examined, the rhabdom does not reach the basal membrane, but stopping abruptly just short of it, leaves an interval which is partly occupied by a highly refractive chitinous body which is a development of the tracheal system. Of this structure, which has been observed but hitherto incorrectly interpreted, I shall have more to say later. As regards the relationship of the rhabdom to the retinulae, most observers are of the opinion that the former is really a complex structure formed from the secretion by each retinula cell of a chitinous rod along its inner surface, and I am inclined to support this view. In more primitive eyes the rhabdom is incomplete and irregular and seems to be little more than a supporting structure. In more highly developed eyes it would appear to be of optical importance. In addition to the structures already mentioned we find in the eye several series of cells containing pigment granules. Their precise number and arrangement varies greatly in different eyes. In *V. urticae* there are two very conspicuous cells occupying the space between the apex of the cone and the outer ends of the retinulae; they form a dense black collar round the cone apex and the distal end of the rhabdom. Between the cones there are series of secondary pigment cells which extend processes towards the basal membrane, these meeting similar processes from pigment cells attached to, or extending from, the basal membrane. There are also pigment granules in the retinulae cells, and in or around the nerves and nerve cells beneath the basal membrane.

It has already been stated that the retinulae cells extend backwards to the basal membrane. The latter is perforated, and through the openings there pass eight nerve fibres, one to each retinula (Pl. II, fig. 1, *n.*). Below the basal membrane these nerve fibres (Pl. II, fig. 4, *n.*) are arranged more or less symmetrically round a large nucleated cell through the centre of which passes a small tracheal tube (Pl. II, fig. 4, *t.*). Passing backwards into the head, these nerve fibres are seen to occur in bundles, each bundle containing fibres appertaining to more than one set of retinulae. The bundles are separated by what appear to be large spaces. These are the lumina of a tracheal network lying horizontally in this part of the eye. Below this layer are several well-marked strata of nerve tissue, notably three ganglionic bodies named by Hickson (Quart. Jour. Micr. Sci. p. 215, etc., 1885), counting from within outwards, the "opticon," the "epi-opticon," and the "peri-opticon." In the peri-opticon the individuality of the ommatidia seems to be preserved, since transverse sections show a more or less regular geometrical arrangement. (See Pl. II, fig. 3). One might fancifully compare it with a telephone switch-board in which all wires or nerves arrive at their proper sockets, though traversing the intervening space, the tracheal area, in apparently haphazard bundles.

Beyond this area I have not so far attempted to trace the course of the fibres, since in the depths of the brain or ganglia the phenomena of sense transmission and perception constitute more of a psychological than a physiological problem, and a study of the inner ganglia is not calculated to throw much light on the visual capacity of the insect.

I have already spoken of a highly refractive body lying at the inner end of the rhabdom. Jonas (Zeit. Wiss. Zool. 1911) seems to have been the first to notice this, and strangely enough observed it in only one species of butterfly. He gives a small text figure and states that he is unable to offer any explanation of it. I have observed it in all the butterflies I have examined, and have studied it especially in *Vanessa urticae* and *Ganoris brassicae.* It is, as above stated, a part of the trachaeal system and has a somewhat remarkable structure. There passes through the basal membrane to each ommatidium a fine trachaeal tube (see Pl. II, fig. 1, *t.*) which immediately increases considerably in diameter, and the usual spiral thickening of its walls can be distinctly seen. This widened portion of the tube contains the refractive body already referred to. Judging by the manner in which it stains it is strongly chitinised. In longitudinal section it is cylindro-conical (see Pl. II, fig. 1, *tf.*), but in transverse section it is cruciform. Fig. 5, Pl. II shows a transverse section of four ommatidia, passing through these bodies near their basal or outer (distal) ends. It will be seen that the four arms of the cruciform section come outwardly into contact with the widened portion of the trachaeal tube, so that four spaces remain. A little higher up, fig. 6, each of these four spaces is divided into two, so that eight spaces are now seen, and these are the lumina of the eight trachaeal tubes which shortly afterwards pass outwards to the surface of the ommatidium and extend forwards towards the corneal layer, ending blindly not far from the crystalline cones. A similar arrangement appears in *V. io* and probably in other *Vanessidae.* In *G. brassicae* the structure is different. Instead of the conical body there is a thick chitinous septum which divides the trachaeal tube into two divisions only, and these pass forward to be again divided into two, but at a higher level than in *V. urticae*, ultimately resulting in only four trachaeal tubes. We may, I think, conveniently call this structure the "trachaeal distributor."

I have already pointed out that the nerves pass through the basal membrane into the retinulae or visual cells. They can still be seen in transverse sections, as eight small circles lying outside the eight branches of the trachaeal system (Pl. II, fig. 6, *ret.*). Negative results in research are rarely satisfactory, and a recital of the efforts I have made to trace the course of these nerve fibres would make long and profitless reading. Thousands of preparations have been made, and various processes which seemed to be indicated have been tried in vain, and I am forced to the conclusion that the nerve does not continue as fibrils into the body of the ommatidium, but that the retinulae are themselves merely large elongated nerve-end cells. Workers on the Crustacea claim in certain cases to have observed nerve fibrils passing from the retinulae horizontally into the rhabdom. So far as my researches go no such structure can be seen in the eyes of butterflies, nor in those of many other insects which I have examined. It will be seen later that certain other workers claim to have seen nerve fibres in various positions, such as the rhabdom and in and around the cones. I have repeated their methods and experimented with many others, but I have never succeeded in tracing the nerves as recognisable fibres further than a short distance beyond the basal membrane. That they do undoubtedly pass through that membrane there is no question whatever, and this fact should be remembered in connection with Lowne's theory to be mentioned later.

Some time after I had arrived at these conclusions in regard to the nature of the retinulae they received apparent confirmation by the work of Domingo Sanchez on the development of the retinal elements in *G. brassicae* (Trab. del Lab. de Investig. Biol. de Madrid, 1916–17).

My attention was called to this work by my friend Mr. J. Bronté Gatenby of the Department of Physiology at Oxford. Sanchez worked on the pupa of *G. brassicae* and succeeded, apparently by Cajal's modification of Golgi's silver chromate impregnation, in demonstrating the purely nervous nature of the retinulae cells. The process is very capricious in its action, and though I had already tried it without result, I made still further efforts, and after a time succeeded in obtaining a differentiation of the retinulae cells indicating their nervous nature.

The optical and primarily receptive layers are evidently to be sought between the basal membrane and the corneal layer, and having noted the general structure of the eye, we may now proceed shortly to review some of the theories which have been advanced in regard to the method and quality of vision of which such an eye may be deemed capable.

The theory which is at the same time the oldest and most generally accepted is that of Müller (Zur vergleichenden Physiologie des Gesichtsinnes der Menschen und der Thiere, 1826) and may be freely translated as follows—

"If light from a particular part of the object can only reach a particular part of the retina, all other parts of the retina will be excluded from this particular light, and so an image is formed. This happens in the composite eyes of insects and Crustacea by means of the cones which lie between the corneal facets and the fibres of the visual nerves, united to each at their extremities and clothed laterally with pigment. Each of these cones peripherally placed round a convex nerve mass passes, to the individual nerve endings with which it is united at its apex, only that light which falls directly through the axis of the cone. All other rays emanating from the same point and falling obliquely on the cornea will fail to reach the lower extremity of the cone and so will not come to the perception of the other fibres of the visual nerves. They will be absorbed, if they fall obliquely, by the pigment-covered walls of the cones, these being transparent only in their axes."

Further :—"The convexity of the corneal facets will guide the light in the direction of the axis, and cause a greater concentration in the depth of the eye. So it may happen that the whole light passing through the cone will be concentrated at the apex where the nerve fibres are attached, in the form of a point, whereby the brightness of the image must be much increased. The refraction of the outer surface of the cornea is, however, not so great that it can form a special small image for each facet. If it did no image could be produced, for if one were formed in the focal distance of the lens, it would necessarily be reversed. Not the whole field would be reversed, but the picture formed by each of the facets respectively and unnaturally. As also the facets in the compound eyes of insects frequently show little or no convexity, we can attribute to the peripheral convex surface no other function than the concentration of the light towards the pointed apices of the cones."

This is what is known as the "mosaic" theory of the sight of the compound eye, and may shortly be enunciated thus.

Each facet registers on a sensitive layer a spot of light corresponding in quality to the average of the light reflected, normally to the facet, by that part of the object within the facet's field of view. Hence an erect image will be formed made up of such spots of light in the form of a mosaic. Müller was of course mistaken in stating that the facets could not form an image.

The first to throw doubt on Müller's theory was R. Wagner (Archiv. f. Naturgesch. p. 372, 1835), who considered the sheath of the cone as the true nerve expansion. Will (Leipzig, 1840) regarded the compound eye as an aggregate of simple eyes. Gottsche (Beit. sur Anat. u. Physiolog., etc., Müller's Archiv. p. 483–92, 1852) reobserved the images formed by the facets of an insect's eye with the inside removed, and calculated the focal distance of the image. He considered that his work disproved Müller's theory, and certainly it was the cause of its temporary displacement. Leydig in various papers expressed the view that the cones were the nervous elements, forming with their thread-like continuations a perceptive element comparable with the retina of vertebrates. He thought all the small images were in some way conveyed to the brain and combined into one large picture. Claparède (Zur Morph. der Zusamm. Augen, etc., Zeit. Wiss. Zool. p. 191, 1859) points out that Müller's theory makes the definition of the object dependant on the number of the facets and states that bees can see the hive entrance at great distances. It hardly requires Grenacher's refutation to remind us that there is no proof that bees can *see* the hive any more than that carrier pigeons can see their pigeon-house, and indeed we know from many experiments that bees do not return to the hive door by sight, since they will return infallibly to the place where the door *was* if the hive be turned round. Claparède suggests that each facet sees a definite image and the view is made up of the sum of these images, the physiological difficulty of multiple inverted images being in his opinion no greater than in the case of several simple eyes. He regarded the cone as an optical and percipient element combined.

Ruete (1861) thought that not only the axial rays affected the nerve elements but many rays affected many neighbouring elements. Here we seem to have an anticipation of Exner's "superposition image." Dor (1861), examining the subject from an optical point of view, made out that the image was formed at the hinder end of the cone and condemned Leydig's theory of the nervous constitution of that body. He regarded the cone sheath as the retina, and in reply to the difficulty of its shape for receiving a picture points out that the human retina is not truly spherical.

Schültze (Untersuch. uber zusammenges. Aug. Bonn, 1868) held that the mosaic theory was physically untenable, as also Leydig's view of the nervous nature of the cones, these latter being in his view a purely dioptric apparatus for the production of the image. Schültze's monograph is one of the most interesting of the older works on the compound eye, since it enters into great detail on the question of the nerve distribution. According to that author the central rod or rhabdom of the ommatidium is the nerve rod, formed of several fibres in a common sheath. He claims to have seen these fibres very distinctly. They are said by him to have a laminated structure as though made up of a great number of small plates transversely superimposed. At the outer or distal end they divide and enter the cone, to the number in some cases of eight, being then apparently lost in the substance of the cone. Schültze's figures and descriptions are very convincing, and one feels almost inclined to believe that he saw the structures he describes, though Grenacher, who spent years in examining these eyes, does not appear to have found the nerve fibres, and indeed professes to doubt their existence. He states that Schültze found them only in a very few cases, and himself confessed that he was unable to find them in the majority. Boll (1871) pointed out the unimportance of Leuwenhoek's images, reobserved by Gottsche, these being an incidental consequence of the lenses of the facets. He also pointed out the lack of accommodation in the insect eye, and the impossibility of combining an endless number of images into one picture.

In 1879 appeared Grenacher's great work on the Arthropod eye (Untersuch. uber der Arthrop., etc., Gottingen, 1879). For beauty of illustration this work has probably not been surpassed. It will be necessary to review at some length that author's conclusions. In the course of his introduction, from which I have extracted part of the foregoing summary, he remarks that the perception of a number of inverted images need not at once be dismissed in view of the simple Arthropod and the Vertebrate eye, but its probability will depend on the nature, and especially on the number, of the percipient elements belonging to each corneal facet. If, where the light rays fall, there be only a single percipient organ, it must either perceive only a small portion of such picture, or else, if large enough to take in the whole, it will only record a mixture having the general luminosity of the picture. The difficulty of the reversed image is not in his view a good reason for rejecting it, since spiders with six to eight simple eyes, certain water-beetle larvae with twelve, and other creatures must have inverted images.

He proceeds to classify the two main theories as first, Müller's theory of mosaic vision, and second, "the little picture theory." Müller's theory provides that only a single perceptive element occurs behind each facet, one nerve element being joined to each cone. In opposition thereto the picture theory will be upheld when a multiplicity of such elements, serving as a retina, can be demonstrated. In all fairly well-developed visual organs in the animal kingdom are found structures of a quite specific kind, the rods, in a wide sense, which are to be regarded as the percipient end organs. In the simple Arthropod eye, and especially in the stemma of insects and spiders, these rods have been recognised. In their main agreement with those of other animals we must claim for them the same signification, the more so since other retinal elements which could be substituted for them are sought in vain. If we accept the projection on the retina of, for example, a spider's eye, of an inverted image, we must also agree that the external object can only be distinctly seen when its rays come to a focus on the rod-bearing region of the retina. For the sight with equal distinctness of objects at varying distances, the vertebrate eye possesses an accommodation or focussing apparatus of which there is no trace in the Arthropod eye. It may perhaps find a partial substitute in the relatively great length of the rods, so that distant objects whose images fall more on the distal ends of the rods, act more on those ends, while nearer objects focussed more in the depth of the retina may specially stimulate the hinder end. I may here remark in parenthesis that this remark has been made by other investigators, as for instance Patten (*vide infra*), and Avebury has raised the objection that the nerves which are first reached by the light would surely be affected by it. As against this objection, it may be urged that in our own experience the attention is more easily focussed on a defined image than on a blurred one, and thus the perceptive power might act in a selective manner. We shall see later, however, that probably neither action is called upon in the perception of the image. Grenacher further points out that the image projection must take place in any case only a short distance behind the distal ends of the rods, for it is here that they are surrounded by pigment. He considers that it is for obvious reasons established that the physiological region of the area of light perception lies between the distal and proximal ends of the rods. The same applies to the compound eye. In "acone" eyes * of *Tipula* and *Ctenophora* the light perception is associated with the seven rods, of which, especially in the latter, the central is much longer than the peripheral, so that the central must have a deeper zone of perception. He then considers those facetted eyes in which the central rod is drawn out into an axial rhabdom, as in Orthoptera, Hymenoptera, Lepidoptera, etc., where the rhabdom is extended into the whole length of the retinula. In these the sectional area is reduced to a minimum, namely the cross section of the rhabdom. Hence it reaches a very considerable depth, and there is nothing to prevent the nervous stimulus acting throughout its entire length. The visual area of the single facet will be reduced the more it departs from the structure of the simple eye. As to the acuity of vision we may come to some conclusion, in for example the spider's eye, by taking into account the distance apart of the percipient elements in different forms. An eye with a great number of small rods on the retinal surface will see more clearly than one sparsely provided. Thus the front eye of *Epeira* will surpass the hinder in this respect, for the former has an incomparably greater number of rods than the latter. On the contrary, the posterior eye has a larger visual field than the anterior. In the compound eye we may compare the number of elements in the retinulae. *Dytiscus* has only four, *Melolontha* seven. Whether or not the former is compensated by a smaller field, we know that the water-beetle is actively voracious and gives the impression of having a greater visual power than the cockchafer. The discovery of a single perceptive element behind each facet would have been overwhelmingly in favour of Müller's theory, but since we know there are more, it remains to ask whether this fact invalidates Müller's theory.

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* Grenacher divides Arthropod eyes into "acone," those which have no crystalline cones or any substitute for them; "pseudocone" eyes, those which have in place of the cone a more or less cylindro-conical membrane with fluid or semifluid contents; and "eucone" eyes, those which possess a true crystalline cone.

If Gottsche's image theory is to be supported it must be true for all facetted eyes; furthermore the image must be projected in the plane where the percipient elements lie, and there must be a retinal layer with many percipient elements to receive it. The formation of a reversed image will depend on the spherical surfaces of the refractive media acting as lenses. This condition is in most cases supplied. It is not to be excluded that the cones may serve this purpose through their convex anterior surfaces. The second condition demands that the image shall be projected where we know the percipient elements to lie, and behind the cones. The Gottsche experiments demanded that the image should pass unaltered through the cone to where the sensitive layer must lie. The material used by Gottsche was very ill adapted to illustrate the effect of the cones, since his flies were insects with pseudocone eyes, the cones of which must have been inevitably destroyed, and, shortly, the experiments do nothing more than show that the corneal lenses act in the same way as would lenses of glass. Grenacher proceeds to recount how he has tried similar experiments with the eyes of nocturnal moths, in spirit specimens of which the internal parts of the eye can be removed and the pigment destroyed by nitric acid. Such an eye so placed as to make it possible to look through it from the back, shows no images at the bases of the cones, but does show sharp images just behind the lenses, where, however, no sensitive elements lie.

The third point which Grenacher brings forward is the question whether the image, if formed, has the necessary area. In general the cone is pointed posteriorly, and therefore we look in vain for a projection which has any size at all. If an image be possible where the rods do reach the hinder end of the cone, it is clearly impossible in those cases where the rods are drawn out to a thread-like structure, often of considerable length. It is further impossible to suppose that an image produced at the forward part could be carried inwards like sound on a string. Grenacher then discusses the question of the existence of a retina, remarking that the reply depends very much on the number of elements necessary to form a tissue which can be so called. He suggests that what is known as the retinula may be regarded as a much-reduced retina having seven percipient elements. In certain acone and pseudocone eyes the perceptive elements are isolated, but it is to be noted that even if each were stimulated, seven elements could not impart to the sensorium an impression of every single object of the picture, nor could a number of pictures projected by neighbouring facets compensate for this deficiency. The difficulty is greater in those more developed eyes in which the rods are fused into a rhabdom, since the picture elements would be greatly reduced in size. From the close approach of the rods it must be doubtful if a single rod responds individually to any one stimulus without the co-operation of its neighbours.

Summing up, he states that in isolated cases there is a lack of the necessary curved refractive medium. In other cases there may be an image, but far behind the eye. In still other cases an image has been seen, but far from where it could be effective. The more proximal projection of this image is precluded by the position of the pigment, added to which there is in most cases the proximal withdrawal of the percipient from the refractive media. In all cases, without exception, the sharpest projection of an image would be without effect owing to the inadequate number of the perceptive elements in each ommatidium, and there is not in any case, he holds, much ground for regarding them as more than a single perceptive entity. The picture theory is therefore untenable. He then proceeds to discuss the path of the light rays entering each facet. The angle at which these fall will determine whether they are to be more or less totally absorbed or reflected. The axial rays will have a simple and direct path to the rhabdom, and these will be the principal ones to affect the percipient elements. He reasserts his opinion that though the rod elements are multiple, they can only be regarded physiologically as an entity. " Each set of rays will come relatively to the position they occupied in the outer world, and this constitutes the erect image of the compound eye." He points out the insufficiency of the facet unit for the reception of the many elements which must be distinguished to form a true image, the strong support which anatomical research gives to the mosaic theory, and the impossibility of understanding an aggregation of thousands of complete eyes, all perceiving images, the more so if each be inverted. He compares the simple and compound eye as starting from a primitive form, which developed on the one hand into an eye with better lens, and more perceptive elements (as in a spider's eye), on the other hand an individual retrogressive movement, compensated by great numbers of elements in definite arrangement and direction. By variation in form and co-operation of the pigment, they effect not, like the simple eye, the collection, but rather the isolation, of the separate rays.

Grenacher undoubtedly makes out a good case for the mosaic theory of vision, both on general principles and in view of the structure of the eye, though we shall see that his theories have to undergo considerable modification in view of more recent research.

Lowne's view (Trans. Linn. Soc. Zool. ii, pt. ii, p. 389, etc., 1884) that the insect retina lies behind the basal membrane merits little consideration in view of our present knowledge. It is largely based on the assertion that there is no evidence that the nerves pass through the basal membrane. It is difficult to understand how the author could have made such a statement had he examined even a moderate number of sections. Moreover, as will be described later, we can under certain circumstances see the image in an insect's eye, and that image certainly does not lie behind or even near the basal membrane. Hickson (*l.c.*) treats mainly of the eye of the Blow-fly, and more particularly with the nervous structure of the ganglia. He considers that the balance of opinion is in favour of regarding the retinulae as the true nerve-end cells. He states that the end elements of the human eye are only ·004 mm. apart, whilst the corresponding distance in *Musca* is ·01 mm.

Patten's work (Eyes of Molluscs and Arthropods, Mittheil. a.d. Stat. zu Neapel. V. 6, p. 542, etc.) has met with no general acceptance so far as it concerns the physiology of the compound eye. His main contention is that the cone is the seat of perception. He claims to have seen by his histological methods the nerve fibrillae which pass up the rhabdom, and, spreading out over the cone, end therein in minute horizontal branches. He is emphatically certain on this point, and one gains the impression that nothing could be easier than to proceed by his methods and see these fibrillae without the least difficulty; nevertheless others, including the present writer, have not succeeded in demonstrating the presence of such fibrils, and there is in fact no real evidence of their existence.

Jonas (*l.c.*) describes and figures the structure of many Lepidopterous eyes. In his description of the structure of the eye he insists on the transversely laminated structure of the rhabdom, which he says is quite easy to see. The writer cannot agree with this statement. An apparent transverse lamination of the rhabdom is occasionally seen in osmic acid preparations, but as a rule it is not visible. Whether the rhabdom is actually laminated or not, I have been unable to decide. Certainly in many cases the fine pigment granules when very slightly out of focus have a tendency to suggest transverse lines, and I feel certain that in some cases at least this appearance has been thus misinterpreted. Jonas failed to discover any nerve fibrillæ, though in cross sections of the retinulae he saw clear spots which he thought might be sections of nerves. He quotes Wagner as describing how in *Sphinx atropos* "the nerve threads or visual nerve bundles surround the apex of the cone like a calyx, passing thence to its anterior surface, and reaching the cornea; the nerve forms a true retina which surrounds the cone like a sheath." Leydig, as he says, took the same view, and he quotes Schültze's minute description of the nerve fibrils entering the cone and surrounding the apex in a cup-like fashion. He then states:—

"With the help of the apochromatic objective I have come to precisely the same results. . . . One almost gains the impression that the old authors were right in that they maintained that the cone sheath extends as a nerve-rod sheath as far as the basal membrane, but a definite opinion cannot be formed until entire proof has been obtained by the study of development."

It may be noted that these views support those of Patten referred to later.

Jonas, though asserting that he has come to the same conclusion as Schültze in regard to the nerve terminals in the compound eye, does not figure them and also states that he could not find them. The value of his observations is somewhat discounted by a very curious and isolated observation. He describes a "cigar-shaped structure" at the base of the rhabdom which he appears to have seen only in *Coenonympha pamphilus*. A small text figure shows the object as attached to the base of the rhabdom by a thread, and he states that he has no explanation to offer for the structure. Why he should have seen it only in *C. pamphilus* is difficult to understand, as a homologous structure is so obvious in *V. urticae*, *V. io*, and other diurnal Lepidoptera that it is a prominent feature in any good section. I have already described this feature and indicated its true nature as a part of the tracheal system. Kurt Bedau (Zeit. f. Wiss. Zool., xcvii, 1911 : Facettenauge der Wasserwanzen) states that his researches into the innervation of the retinula have not had much result. Even with a $\frac{1}{16}$-inch apochromatic and compensating ocular he has not been able to trace in the ommatidia the nerves which pass thence through the basal membrane. He has only been able to see with certainty that the number of nerve fibres corresponds to the eight visual cells. He criticises unfavourably Patten's work and expresses the view that what that author took for nerve fibrillae in the crystalline cone were the intensively stained plasma edges of the four cells of the cone. Many other authors have dealt with various aspects of the subject, but with one exception I have probably given a sufficient resumé of previous work to illustrate the difficulty and complexity of the insect eye. The exception referred to is the work of Prof. S. Exner (“ Die Physiologie der facettirten Augen von Krebsen und Insekten. Leipsig und Wien, 1891). To Exner falls the credit of having demonstrated experimentally the existence and nature of the image in the facetted eye, or at least in certain types of that organ, and it is my intention here to set forth the conclusions arrived at in that admirable piece of research. It is the custom of many writers to quote from foreign works in the original, but while the practice may relieve them of any errors of interpretation, it is of little assistance to those readers who may not have had the opportunity of acquiring a knowledge of the languages in which such quotations are written. Exner's work is of such importance, and the only English summary I have seen (“ Senses of Insects,” Forel; Eng. Trans., Yearsley. London, 1908) so inadequate, that I feel justified in endeavouring to give a more complete account of it than has hitherto been attempted.

Exner first experimented with the eye of *Hydrophilus piceus*, and found that in such eyes the refraction of the rays by the dioptric portion is of a complicated character, due to the fact that the facets and cones are not homogeneous bodies, but have a refractive index which continually decreases from the axis to the outer wall. This form of refractive body he calls a lens cylinder.

In order more easily to explain the action of such an apparatus I have made the two diagrams on Pl. II, which are similar to those given in Exner's work. Fig. 7 represents a lens cylinder, the actual length of which is the same as its focal length. Now the rays emanating from some external point, and represented by the lines *cd*, *ef*, are made to converge by the refractive action of the medium so that they come to a focus at the base of the cylinder. Similarly rays from some other point, represented by *c′d′*, *e′f′*, come to a focus at the same level, and an inverted image is formed at the base of the cylinder. A peculiar difference between this action and that of a lens is, that whereas in the latter the central or chief rays, *ab*, *a′b′*, emerge at an angle, in the lens cylinder the chief rays emerge parallel. Now in the case where such a lens cylinder is twice as long as its own focal length we have the effect diagrammatically shown in fig. 8. Here the inverted image occurs in the middle of the cylinder, and the lower half of the cylinder acting in the same way, rays which enter the cylinder on the right, as *c′d′*, *e′f′*, emerge again on the right, and the image is thus erected. In insect eyes both these optical effects occur with apparently varying results. According to Exner two kinds of image are formed in the compound eye. The first is the superposition image. A very perfect example of this image is furnished by the eye of the male glow-worm, *Lampyris noctiluca*. In this insect the visual rods or retinulae do not extend forward so as to touch the ends of the cones, but are separated therefrom by a small space, filled with what in life is a doubtless transparent tissue. The pigment between the cones is not stationary, as in some other eyes we shall examine, but is capable of movement backwards or forwards according to the amount of light entering the eye. Thus if the light is weak the pigment moves forward towards the corneal layer, and exposes a larger portion of the apex of each cone. Now, as Exner has shown, the corneal facet and the cone in this beetle act *together* as a lens cylinder of twice its own focal length. Hence the rays emerging from the cone apex form a little *erect* image of that part of the visual field opposite its own particular facet. If the corresponding visual rod were adjacent to the cone apex and separated from other visual rods by a sleeve of pigment, such rod would receive only the stimulus proceeding from its own facet unit (lens and cone). But we have seen that not only are the visual rods at some distance behind the cones, but also the pigment is, under weak light conditions, drawn forward so as to expose a considerable part of the cone apex. The result is that each visual element receives not only the stimulus from its own facet unit, but also that of the peripheral rays from neighbouring facet units. The images it receives from such rays are superimposed upon those thrown from its own cone and lens, and thus the image is made brighter and more of the light entering the eye is utilised. This is the true superposition image. If the external light be strong, the pigment moves backwards like a dark sleeve, cutting off more and more of the peripheral rays, thus decreasing the luminosity of the image, without interfering with its clearness. The pigment, in fact, has a similar function to that of the iris of the vertebrate eye.

Owing to a peculiarity in the morphology of the glow-worm's eye this image can be easily seen. The cones are so firmly attached to the facet lenses that in a fresh eye all the nervous apparatus can be brushed away from the inside of the eye, leaving a little hemispherical shell consisting of the cornea with its cones in position.

If this little shell be mounted on a small drop of dilute glycerine (to reproduce the refractive effect of beetle blood) on a glass slide, and then viewed from the back through a medium-power objective, and using the plane mirror, any object placed between the corneal surface and the mirror can be distinctly seen as an *erect* image, allowing of course for the fact that it is inverted again by the microscope itself.

The beauty and sharpness of this image are remarkable. If the microscope be tilted up, the mirror removed, and the whole apparatus pointed towards a distant landscape, trees and any other objects in the field of view are all seen with surprising precision.

Exner succeeded in photographing such an image in an allied species, and I have repeated the experiment with the result shown on Pl. IV, fig. 2, which is a portrait of my friend Prof. Poulton taken through a glow-worm's eye.

It has, of course, lost much of its sharpness. The practical difficulties in making such a photograph are considerable. The exposure is prolonged, and whilst it is taking place the water is evaporating from the glycerine, altering all the time the refractive index, and thus affecting the clearness of the image. Moreover, small as the picture is, it is an enormously enlarged view of the optical image which in the actual eye has an area calculated roughly at ·154 sq. mm. Exner has given an elaborate mathematical proof of the formation of this image, but I have neither the space nor the mathematical knowledge to deal with that aspect of the matter.

It should be noted that the picture is not a mosaic at all, but a continuous image, and doubtless perceived as such by the insect. Those who have examined the beetle will have noted how the whole head, including the eyes, is completely overshadowed above by an opaque chitinous projection. Evidently the insect can only see forwards and downwards. No doubt the natural eye shade it possesses helps to give it an additionally acute vision for objects on the ground, amongst which is to be found its main object in life, its mate.

Exner points out that two features easily recognisable in the eyes of insects are, when present, especially adapted to the production of a superposition image. These are, first, the movement under varying light intensity of the "iris" pigment, and secondly, the existence of a space between the cone apices and the visual rods, or the thickest part of them.

Superposition images are found in all those insects which have to make the most of feeble light, and hence are specially characteristic of nocturnal and crepuscular Lepidoptera. The exclusively apposition image, on the other hand, is found only in diurnal insects, such as butterflies, flies, and dragon-flies. This form of image approximates very closely, according to Exner, to that of the original mosaic theory of Müller, in that the individual "image" produced by each facet unit is of less importance as an image than as a spot of light.

It is at this point that the results of my own researches in the case of butterflies, at any rate, lead me to conclusions markedly different from those of Exner; but I will speak of these later. To continue, Exner describes how he cut off slices of the eyes of various insects which have the retinulae adjacent to the cones. Having obtained such a section as, when mounted in the manner already described, showed a series of small dots of light corresponding to the cone apices, he proceeded to endeavour to study the image there formed.

In an ordinary humble-bee the light dots were so small that when he used two light spots as objects the brilliancy of the light dots was increased, but the two light rays could not be separated. It was thus hopeless to expect to see an image. On the other hand, he succeeded in the case of *Calliphora vomitoria* in seeing the two dots separately, and in proving that the image at the cone apex is an inverted one. By measuring the distance between the two light images, and then wiping away the cones, and measuring again, he found that the distance was practically the same, from which he concludes that the cone in this insect has an inappreciable optical effect. He admits his surprise at this result. The main conclusion is, however, that the images produced by the facet units in diurnal insects having apposition images are inverted, and therefore the picture presented to the percipient layer of the insect's eye is made up of a multitude of inverted images, or alternatively of mere light spots. One must conclude from this that the elements composing the whole picture are not, as images, of any value, but merely act as light spots of the average quality of that emanating from the portion of the field recorded by each facet.

If this be so, then the apposition image is, as an optical performance, very inferior to the superposition image, although nevertheless produced by a much more highly developed and intricate optical apparatus, at any rate in the case of eucone eyes.

I have here endeavoured to give as concise an account as possible of the image formation in the compound eye as set forth by Exner. There is much more in his book, which is a record of by far the most complete research yet made on the physiology of the compound eye, and is of a value which even the occasional profound obscurity of expression peculiar to the German language fails entirely to hide.

AUTHOR'S EXPERIMENTS

It remains to describe some of my own experiments, and to record the extent to which they confirm or refute previous results. I have already stated that I was able to see and photograph the image in the glow-worm's eye, and my observations on that insect convince me that there is no doubt whatever of the correctness of Exner's conclusions, both practical and theoretical, in regard to the nature of the superposition image.

The problem of the apposition image is much less easy to solve. Exner had already utilised the idea of freezing the eye in order to maintain the cones and other structures in their relative positions. The same idea occurred independently to my friend Prof. Poulton, though with the additional complication of maintaining the eye in a frozen condition during examination. A large dragon-fly's eye seemed to promise the greatest facility in handling, and I therefore designed and constructed a somewhat elaborate apparatus for carrying out the experiment. A special hollow stage was made, having a central aperture into which were fitted type-metal blocks pierced through the centre for light, and accurately cast to fit the eyes of various large species of dragon-flies. Small copper pipes attached to the stage conveyed and withdrew a freezing mixture of ice and ammonium chloride, which was kept circulating by means of a small gunmetal force-pump actuated by an electro-motor. The lower side of the freezing stage was fitted with a glass box having an annular space containing calcium chloride, so that the corneal layer of the eye should be in perfectly dry air and free from the obscuration caused by condensation. It was hoped by these means to maintain the eye in a frozen state whilst the nervous and other tissue was gradually brushed away from the back, until the level of the cone apices was reached.

In its primary object the apparatus was entirely successful, the eye being completely frozen in a few minutes. I may also mention that both carbon dioxide and sulphur dioxide were tried as alternative freezing media, but the method described proved much superior to either.

Unfortunately the results obtained with this apparatus were not commensurate with the time and labour expended in its construction and use. With the eye of *Libellula depressa* the apices of the cones could be seen as bright points of light, but no image, inverted or erect, could be observed. A pencil or other object moved in front of the eye caused a shadow, not well enough defined to be called an image, and this shadow moved, as one would have expected, in the same direction (allowing for the effect of the microscope) as the movement of the pencil. A similar experiment with an eye of *Hemaris fuciformis* gave a rather clearer shadow or image. In general the observations, which were numerous, merely confirmed the results obtained by Exner with a large dragon-fly. The apices of the cones are so small that by the means at our disposal it is very difficult to see the image, if any, which occurs there. Nevertheless on another occasion, having succeeded in obtaining a portion of the cornea of a *Libellula* with the cones still attached, I could see first of all the usual sharp inverted image caused by the corneal facet, and focussing backwards, there appeared to be, in the neighbourhood of the cone apices, a much smaller, much less distinct image, still *inverted*. I have already mentioned that in the blow-fly Exner claims to have seen at the cone apices the two light points used by him as objects, and to have satisfied himself that the image at the apex is an inverted one. I have examined flies' eyes in the same way, and though the presence of an image at all, beyond that of the corneal facet, seems rather doubtful, there certainly seems no evidence that the cone reinverts the corneal image.

We must, I think, conclude that in flies and dragonflies the picture presented to the perceptive elements is a mosaic of light spots but little if at all modified from that supposed by Müller. This may seem a disappointing performance for the enormous and complicated eye of a dragon-fly, but we must not forget the relative size of the eye. The sharpness of the view obtained with a mosaic of light dots obviously increases in proportion to the number of the elements making up the mosaic. If the rods and cones of the vertebrate eye are the separate elements of the visual apparatus, presumably each is stimulated by a minute bundle of rays which is in itself merely a light stimulus and not a picture, so that our own vision may be said to be a mosaic with exceedingly small elements, and the difference between this and the image of the facetted eye may be roughly compared with the difference between a half-tone block made with the very finest screen and the corresponding picture as represented by the very coarse screening used in the common newspaper pictorial reproduction.

Both flies and dragon-flies have pseudocone eyes, *i. e.* the cone is merely a fluid body, and not, as in butterflies, a true "crystalline cone." Presumably the latter is a higher development, whilst the former has persisted, at least in the dragon-flies, from great antiquity. It is when we turn to the butterfly eye that my observations do not confirm Exner's conclusions as to the manner of formation of an apposition image. Here we have to do with a eucone eye, and I am convinced that in butterflies at least there is at the apex of the cone a tiny *erect* image of that part of the field appertaining to each facet unit. I first saw this image in an eye of *Gonepteryx rhamni* which had been hardened in strong formol for twenty-four hours. A very thin slice was cut off and mounted on a drop of dilute glycerine on a cover slip and the whole set up on the microscope so that the objective was applied to the back of the section. Focussing down, in spite of the very small openings corresponding to the cone apices, the usual inverted image due to the corneal facets could be seen. Focussing up this image gradually disappeared and was replaced by a much less distinct but nevertheless erect image, *i. e.* an image of a pencil or similar object moves the same way as the object itself is moved, making due allowance for the reversal due to the microscope.

This peculiar effect is by no means easy to see. It is not due to the combined action of a large number of facet units, but is peculiar to each facet. One must have a very favourable section, and frequently before the necessary delicate adjustments are made the minute drop of dilute glycerine has suffered from the evaporation of the water, and all has to be done over again. For some time after I first saw it I was unable to get it again, and began to think I had been deceived. Since then, however, I have repeatedly observed it in the eye of *V. urticae*, and I am convinced that the rays of light which reach the sensitive layers of the butterfly's eye do so in their proper relations corresponding to their respective positions in the outer world. Let us now consider for a moment the difference which this fact may make in the acuity of the insect's vision. I have drawn on a large sheet of paper a curve representing a section of the corneal layer of the eye of *V. urticae*, and marked it off into as many divisions as I found facets in an actual section. Then I drew across the paper straight lines each perpendicular to an imaginary facet, and these lines formed a great sheaf radiating from the eye, the space between the lines of course increasing as the distance from the eye increased. Then a line two inches long, drawn two inches away from the eye, and at right angles to the centre line of the sheaf, would represent an object two inches from the insect's eye. Such a line cuts across a number of the other lines, and this number represents in linear fashion the number of facets which would be engaged in viewing an object two inches long, two inches from the eye. Another line of the same length but twelve inches from the eye cuts across a much smaller number of the lines, since here they are wider apart. From this diagram I obtained a number for the facets engaged in viewing an object two inches long but twelve inches away from the eye.

I was thus able to calculate approximately the number of facets of a tortoiseshell butterfly's eye which would be engaged in viewing another of the same species at distances of two and twelve inches respectively. I then made a drawing of the butterfly and divided it off into small areas equal to the number of facets at two and at twelve inches, and assuming that each facet unit conveys, not an image, but only a spot of light of the average value of that part of the field which it covers, I built up a drawing of the butterfly with spots of colour in number corresponding to the small areas into which my first drawing had been divided. I did this for both cases, the two-inch and the twelve-inch, and the result is shown on Pl. III. Fig. 1 shows the tortoiseshell butterfly as it appears to our eyes, fig. 2 the same as it may be supposed to appear if made up of little dots of light corresponding to the number of facets engaged at a distance of two inches, and fig. 3 the same at a distance of twelve inches. I have furthermore endeavoured to represent the appearance of the same butterfly at twelve inches, assuming that each facet unit records a sharp but inverted image of its own field of view. For this purpose I cut a drawing of the butterfly into hexagonal pieces each representing a facet view, and then turned them all upside down. The result is shown at Pl. IV, fig. 1. The effect is peculiar, and the reader may derive some amusement from trying to decide whether Pl. III, fig. 3, or Pl. IV, fig. 1 looks most like the original butterfly, for if we accept the mosaic theory, either as spots of light or as clear inverted images, one of these two pictures must represent the sort of view from which the sensitive layers of the insect's eye obtain their impression.

That these insects are extremely short-sighted every one who has observed them will agree. We know what a conspicuous object a white butterfly is. We can see it at great distances, and yet two white butterflies will often pass within a few feet of each other without either being apparently conscious of the other's presence. We know how readily one white butterfly will pursue and investigate another to see if it is a suitable mate, but I have never seen this kind of flirtation begin from a distance of more than a few feet. Nevertheless, in my view a butterfly's sight is much more acute than the figures on Pls. III and IV would suggest, and for this reason: I believe that the rays of light entering the facet unit are not recorded as a light spot, or as an inverted image, but as an erect image, the whole field of view being represented by a mosaic of little erect images, thus forming a continuous picture. I have already explained how I have actually seen these erect images, albeit with difficulty and not very clearly.

There is one feature of the butterfly's eye which does not appear to be present in dipterous and other pseudocone eyes—viz. the already described *processus corneae.* Now Exner regards the lens and cone *together*, in an apposition eye, as forming a lens cylinder of which the actual length and focal length are the same, hence giving an inverted image. This condition may, and apparently does, obtain in some eyes in which the short cone is closely adjacent to the lens, forming what may be regarded as a physical entity, or where, as appears to be the case in a fly's eye, the pseudocone is of such feeble refractive power as to have little effect on the image already produced by the facet lens.

Now in the butterfly the *processus corneae* lies between the lens and the cone, so that these latter structures presumably do not act together as one lens cylinder of its own focal length. What I conceive takes place is that the lens produces an inverted image (this can, of course, be very clearly seen), the rays from it are collected by the cone, and that is a lens cylinder of its own focal length. Acting on the principle already explained, the cone reinverts the image, passing the rays out at its apex or inner end practically parallel.

From here they pass down the rhabdom and stimulate the retinula cells. The stimulation does not take place on the *ends* of the retinula cells, as, for instance, in the glow-worm's eye, but along the inner edge of each cell throughout its whole length.

Now Grenacher maintains that the retinula cells of each ommatidium, though multiple, can only be regarded as a physiological entity, and if we are to compare the receptive faculty of the compound with that of the vertebrate eye, we must compare the number of ommatidia in the former with the number of rods and cones in the latter.

However this may be in other compound eyes, I hold it to be an error for that of a butterfly. If there are eight retinula cells in each ommatidium of the eye of *V. urticae* I regard them as eight separate elements, the more so since in some species, as, for instance, *V. io*, they are to some extent separated by pigment. Hence the little pencil of light projected down the rhabdom by each facet unit, and having its rays arranged in their proper order and position by the re-erection brought about by the cone, is analysed, and presumably perceived with eight times the accuracy with which a mere amorphous spot of light would be perceived, and similarly one tortoiseshell butterfly may be supposed to see another, at a distance of two inches, eight times more distinctly than as shown at Pl. III, fig. 2. Two factors thus contribute to the better perception of the image, viz. the proper co-ordination of the rays and the multiplicity of the perceptive elements.

One point remains. It has been suggested that there is a difficulty in understanding how light passing down a transparent rod, the rhabdom, can effect the retinulae adjacent to it, since light entering a glass rod at one end emerges only at the other end and not through the sides.

I have submitted this point to Lord Rayleigh, who has kindly assisted me on several occasions. In his reply he points out that this action of a transparent rod is true for the rod surrounded by air, but that in the ommatidium of the compound eye this condition does not obtain.

The physiological continuity of the rhabdom and retinula cells doubtless provides for the due action on the latter of the light stimulus.

TECHNIQUE

Many thousands of preparations of eyes were made in the course of my investigations. Of hardening re-agents

I have tried several. For some purposes the well-known saturated solution of corrosive sublimate in water to which is added 50 % of alcohol was found very good. About 1 % glacial acetic acid may be added if required. Sections thus prepared and stained for twenty-four hours in anilin-water-saffranin followed by a short immersion in a 2 % solution of light green in alcohol, give a very beautiful differentiation of the cones. For showing the peculiar structure of the trachaeal distributor at the base of the rhabdom the ordinary combined methyl blue and eosin (Mann's stain) is the best, and this also gives good preparations of the general nervous arrangement. One of the best fixatives of high penetrative power is "Picro-chlor-acetic acid" made up as follows :—

1 % Picric acid in alcohol	6 parts
Chloroform	1 part
Glacial acetic acid	½

Fix for twenty-four hours and wash well in 90 % alcohol.

The nerve fibres passing from the periopticon to the retinulae are very well shown by Heidenhain's haematoxylin. Potassium bichromate and solutions containing formalin are, as a rule, of very little use, as they render any chitinous parts exceedingly brittle, and the softer parts are also made liable to pulverise at a touch. One of the great difficulties in all insect eye preparations is the pigment. If any fixative containing osmic acid be used all pigment cells are intensified and the pigment cannot be removed. The same applies in great measure to silver nitrate. For depigmentation after fixation the following solution works very well :—

80 % alcohol	2 parts
Glycerine	1 part
Hydrochloric acid	2 %

Sections after removal of paraffin or celloidin or both are put into this solution, and the pigment disappears in a few hours or less.

Buxton (Trans. Ent. Soc., 1917, p. 144) obtained good results with insect brain tissue by putting material into a 1 % solution of silver nitrate in water for ten days in the dark and then washing. The material is embedded in paraffin and sections cut. After removal of the paraffin and hydration of the sections they are placed in 1½ % silver nitrate and exposed to bright sunlight for ten minutes, washed in distilled water, and placed in 1 % gold chloride for two minutes in a bright light, washed again and placed in aqueous solution of pyrogallic acid to complete the reduction.

I have given this process at length because other workers may find it useful for brain tissues. For eye work I have not found it of much service on account of the old difficulty of the pigment cells, which are stained so deeply as to obscure any other structures with which they are in contact.

Methylene blue, Ranvier's lemon juice method, and other nerve processes have been tried, but without any marked success.

A method which promises good results in the differentiation of nerve tissue seems to be the double impregnation of silver chromate already referred to. Like most of these processes it is exceedingly capricious, and too much must not be expected of it. Sometimes nerves in one part of a section will be differentiated, whilst in others they remain unstained. Moreover, the material so prepared will rarely stand the usual embedding processes, and I find the most likely method of seeing the structures required is to tease out on a slide small portions of the tissue and examine them as non-permanent preparations. The material is placed in a 2 % solution of potassium bichromate to which a very little formol has been added, and the tube exhausted of air. The material remains in this solution for about three days, when it is placed in 1 % silver nitrate for two days, then returned to the bichromate solution (freshly prepared) for two days, and finally put back into silver nitrate for two days or more. It can then be washed in 90 % alcohol and examined.

For section-cutting I have used both paraffin and paraffin-celloidin. If chitinous parts are not required, cornea, etc., can be removed after fixation and only the soft parts left. Paraffin sections can then easily be made. For sections including the chitin I have found the following process the most satisfactory.

Fixed and dehydrated material is placed for two or three days in a solution of celloidin in clove oil.* Then transfer the material to a weak solution of celloidin in ether and alcohol, and concentrate to a syrup at about 40° C. Pour into a mould and harden in chloroform vapour in the usual way, and then transfer to a saturated solution of paraffin in chloroform for twenty-four hours. Then place the block in melted paraffin having a melting point of about 55° C. and exhaust with a water air-pump, finally embedding in fresh melted paraffin.

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* Celloidin dissolves in clove oil only very slowly. Many weeks may be required for the solution to become saturated.

This combination of clove-oil celloidin saturation with double embedding was suggested by Dr. C. J. Martin of the Lister Institute. In my experience it is superior to the much-vaunted spirit-soap treatment. The alleged chitin-softening action of spirit-soap seems to me to be much over-rated.

Nearly all my sections were cut with a Cambridge Rocking Microtome, which, except for pure celloidin sections, is quite as efficient as the more complicated and costly instruments.

CAN BUTTERFLIES DISTINGUISH COLOURS?

Before investigating this question and considering such experiments as may be regarded as throwing some light on the subject, it will be as well to make clear the meaning of the question and the necessary limitations of any answer thereto. We know that light consists of vibrations or waves, and since we cannot imagine waves in nothing, and since light reaches us from the stars across illimitable tracts of empty space, we suppose the existence of an invisible, intangible, perfectly elastic medium called the aether, which is considered to permeate the universe and all material substances contained therein. The vibrations set up in this medium by a source of light are of differing wave lengths and wave frequencies, and our own visual organs record different sensations according to the frequencies of the waves which fall upon our eyes. The light we receive on our own retina may come direct from the source of light, or more commonly may be reflected from the surface of some substance upon which the direct light is falling. If the light we receive contains a normal admixture of all the rays of differing length and frequency we experience a sensation which we call "white." It is possible to separate the component rays of white light by passing them through a prism, as in the well-known spectroscope. The rays are bent or deflected from their original course, but all are not equally deflected. Those of the shortest wave length are deflected most, and hence it is possible to project on a screen a band of light, one end of which consists of the rays of shortest wave length, the other of those of the longest, those of intermediate wave lengths occupying the intermediate positions.

We are now, however, aware of a new fact, the band of light is no longer white, but the different portions of it produce in us different sensations which we call colour. Thus the band to a normal eye appears deep red at one end, and changes towards the other end into orange, yellow, green, blue, dark blue, and finally violet. An object such as a flower appears to us to be coloured because its substance absorbs some of the light falling upon it, and reflects the rest. Such colours in nature are rarely pure, *i. e.* they consist of mixtures of reflected rays, thus producing what we term various "shades" of colour. These mixtures of colours can be analysed by looking at the objects through special light filters which entirely absorb certain rays, while allowing the rest to pass unaltered. Some rather unsuspected effects may in this way be obtained. Thus a deep blue lobelia examined through a screen which is impervious to blue rays, looks deep red, showing that its colour consists partly of red rays. Similarly certain forms of pale pink pelargonium when examined through a filter impervious to red, appear bright blue, although we are not conscious of the blue component of the colour when seen under normal conditions.

It may thus be seen that we may be said to possess two separate visual faculties in relation to light. One, the fundamental perception of light as such, the other the capacity for distinguishing, apart from mere luminosity, lights of different wave lengths; and a totally colour-blind person is one who possesses only the former of these two faculties. Such cases are extremely rare, though partial, and especially "red-green" blindness is of frequent occurrence. In one case of total colour blindness or monochromatic vision, instanced by Sir William Abney ("Researches in Colour Vision," London, 1913), the subject had no sense of any colour, and moreover his sensation of luminosity was about one-thirtieth of that of a normal person, and much the same condition was observed in a second example given by the same author. That the two faculties mentioned are in fact quite distinct is shown by a third case in which the subject appeared to have the sensation of green, but little or no fundamental sensation of light.

Having thus explained something of the meaning of colour vision as applied to our own eyes, to what extent can we apply the terms we ordinarily use to the question of colour vision in an insect? Naturally we cannot know whether what we call red or blue appears red or blue to a butterfly, in the same sense as it does to us. We may, I think, leave out of account all philosophical verbiage on the subject of whether an insect is or is not a conscious organism. Consciousness is probably a matter of degree, and though in creatures of lowly cerebral organisation it may be reduced to a condition hardly definable by our limited imagination, some form of consciousness seems postulated in any creature which leads an independent and more or less complicated existence. When therefore we ask, can a butterfly distinguish colours? we mean, does it, as a nervous organism, possess the faculty of distinguishing those differences in the quality of light waves which we speak of as colour, in a sense distinct from their mere luminosity value? With butterflies comparatively few experiments have been made. With other insects such investigations as have so far been recorded have naturally been carried out with species in which a colour sense might be supposed to be of some use in the creature's economy. In nature animals are rarely endowed with faculties which are superfluous to their mode of life, though at the same time we must not too readily assume that any given insect can have no use for a sense of colour, since there are probably few species of the ultimate details of whose life history we have absolute knowledge.

Bees, with their intimate relationships to flowers have naturally prompted a considerable measure of research, more especially as the theory has been advanced, first by Sprengel in 1793, that flowers attract insects, and especially bees, by their bright and conspicuous colours. H. Müller's experiments resulted in the statement that, *caeteris paribus*, a flower will be sought by insects in proportion as it is conspicuous. Wery arrived at similar conclusions. Müller also pointed out that the perfume is a powerful attraction. Many early researches might be quoted, but the methods are frequently faulty and the results inconclusive or contradictory.

Plateau's conclusion that all flowers might be green without their due pollination being interfered with does not seem to me to prove that flowers which are not green gain no advantage from their different appearance. Such observations, however they may affect the question of the origin of colours in flowers, seem to prove or disprove very little in relation to the insect's power of chromatic perception.

Lord Avebury's experiments merit a greater consideration. He experimented largely with bees. In one case he gave a bee a drop of honey on a blue paper, and then three feet away placed a similar drop of honey on an orange paper. After the bee had had two feeds the papers were transposed, but the bee returned to the blue paper. After a while the papers were again transposed, and the bee returned to where the blue paper had last been, and found the orange one. It evidently looked different, as she stopped and made for the blue paper again. The author thus comments on the experiment: "No one who saw her at that moment could have the slightest doubt about her perceiving the difference between the two colours."

The experiment does not, however, really prove that the bee distinguished the colours. A totally colour-blind person might be able to separate blue and orange papers, not by means of their colours, but through their different luminosity. The same author also carried out a rather complicated experiment with honey on slips of glass which had coloured paper attached to them. By changing and removing these and carrying out the experiment many times, he arrived at the conclusion that his bees showed a marked preference for blue, then white, and successively yellow, red, green, and orange.

The order of the colours is peculiar, especially the position of the red. If bees are colour-blind and guided mainly by luminosity the yellow and green should have been the most conspicuous colours, but we have here the red coming between these, a result which would not, I venture to suggest, be obtained with a colour-blind animal.

That insects are *attracted* by the colours of the flowers is very improbable, and the theory that flower colour has been developed because its attractiveness assists in pollination has little foundation. Nevertheless, the colours of flowers may well have been developed as an aid to *conspicuousness*, as opposed to attractiveness. My friend, Dr. Church, who has made a special study of floral mechanism and the visits of insects, fully agrees that a flower which is more conspicuous will be likely to be visited before one which is less so. From the experiments of Forel, Avebury, Plateau and others we have evidence that insects, especially bees, have a remarkable memory, not only for locality, but also for colour. Thus a bee which has been given honey on a blue paper rapidly associated the idea of honey and blue, or whatever sensation the blue colour may convey to it. Lest it should be supposed that bees are specially associated with blue, we may instance another experiment of Lord Avebury. Equal-sized discs of red, yellow, green, and blue were provided, and honey was placed on the red disc. A marked bee was also placed on the red disc. After the bee had fed, gone back to the hive and returned a few times, the red disc was replaced by a blue disc with honey, and another red disc was placed near, but without honey. When the bee returned it went to the red disc and searched for the honey it had been accustomed to find thereon. Nor could it find the honey on the blue disc, though this was close at hand, showing a defective sense of smell. Numerous further experiments showed that bees rarely confuse colours except blue and green. Forel tried the same experiment in the opposite order, when the bee always went to the blue disc, and even to a strip of blue paper, showing that it was not the form which guided it.

More valuable evidence than all these observations is given by Forel when he describes how a bee, fed on blue paper, afterwards sought out and examined all the pieces of blue paper in various corners of the room, in whatever surroundings they happened to be. The latter part of the sentence discounts entirely the mere luminosity value of the blue paper.

Before describing my own experiments which have been made with butterflies, I must briefly review the work of Hess, referred to in the first part of this paper, from which that author deduces the opinion that insects, bees and butterflies included, are totally colour-blind. In attempting to show that his results with these insects are inconclusive I do not wish to detract from the value of his research with other animals, especially those with birds and dyed grain, which are very interesting and ingenious. He experimented with larvae of *Hyponomeuta variabilis* by placing them in a glass vessel with parallel sides, and found that for the most part they crept to the lid nearest the light. If a strong light were arranged in one half and a weak light in the other, they crept into the bright half. When a spectrum of suitable width was thrown on to the parallel-sided glass vessel, they crept into the yellow green. If the vessel were moved so as to bring those in the yellow green into the red, they moved again into the yellow green. With a photometric apparatus consisting of a red and blue lamp the larvae sought the blue, even when to the human eye the red was the brighter colour.

Larvae of *Porthesia chrysorrhoea* crept to the most brightly lighted part. In the spectrum they moved from the other colours into the yellow green. Larvae of *Vanessa io* behaved in a similar manner, and imagines hatched from them were investigated in the same way. In the spectrum the butterflies fluttered out of the red, blue, and violet into the yellow green. When the cage was lighted half with bright red, half with dark blue, the greater number went into the blue. "All my larvae behaved as they must behave if their visual powers are the same as, or similar to, those of a totally colour-blind person. There is nothing comparable to the colour sense of the normal human being." With other experiments he shows fairly conclusively that mosquitoes and their larvae are insensitive to red light, whilst still further investigations show that Chalcids, lady-birds, and house flies tend to move from other colours into yellow green.

Bees were experimented on, first by showing that they were strongly positively phototropic, and then by showing that they moved out of the other colours into the yellow green. Given the choice of blue and red, they moved out of the red into the blue. With the photometric apparatus they preferred the blue to the red, even when the latter appeared to the operator to be brighter than the former. By increasing still further the red light the bees moved into the latter. He concludes from these and other experiments that the bees behaved essentially in the same way as the other insects he experimented upon.

After quoting at considerable length the experiments of Avebury, Plateau, Forel, and others, Hess thus disposes of them :—

"The value of such numerous observations and laborious experiments is discounted by the fact that they have, almost without exception, been undertaken without knowledge of colour physiology. Perusal of the extensive literature bearing on the subject has not disclosed to me a single fact which makes even probable, from the point of view of scientific chromatology, the existence of a colour sense in bees. In my own experiments the bees, like all other invertebrates investigated, behaved as they must do if their visual power were the same as, or similar to, that of a totally colour-blind man. In all the results hitherto obtained in this direction by zoologists and botanists, there is nothing to contradict this."

As to whether the experiments of others, which Hess so ponderously dismisses as valueless, are really so devoid of merit as he maintains, I will leave others to form their own judgment. Let us suppose for the sake of argument that all the accumulated work of Avebury, Forel, Plateau, and others has failed to prove that insects distinguish colours. To what extent does the work of this expert in scientific chromatology prove that insects are colour-blind?

He takes certain insects having a marked positive phototropism, and having confined them in a cage makes the surprising discovery that they tend on the whole to make their way towards the light. Caterpillars and mosquito larvae we should hardly credit with a high degree of colour sense in any case. As to the bees, they showed a tendency to regard a dark blue as more luminous than a bright red, and the peacock butterflies showed the same preference. At the most this only suggests a "short vision" at the red end of the spectrum. Avebury has shown that ants at least are sensitive to the ultra-violet rays which are invisible to us. Why not bees also and even butterflies? Avebury submitted negatively phototropic ants to light from two screens of a colour which appeared the same to the human eye, but one of the screens was made opaque to ultra-violet rays. The ants chose the latter colour to hide under, as it evidently appeared to them the darker.

Hess considers that his insects behaved exactly as a totally colour-blind *person* would have done. Now totally colour-blind persons are extremely rare, and their behaviour under given circumstances is not exhaustively tabulated. But even accepting the very unsatisfactory anthropomorphic comparison, let us see what these "colour-blind" insects did.

To the instinct of a positively phototropic creature, light and freedom are probably closely associated. The imprisoned bees and butterflies presumably responded to that stimulus which guided them towards what in their experience, or nervous reflexes, or whatever conscious or unconscious psychological process we may fancy, indicated escape. I imagine that a human being bent on escaping from a dark cave would make for the opening whose light was of the greatest luminosity, as suggesting the shortest route to the outer world. Such action would not prove him to be totally colour-blind. Hess is at some pains to explain that the existence of colours is no proof that they must have been developed in order to be seen, and calls attention to the colours of such substances as egg yolk, blood, chlorophyl, and the green bones of certain fishes. I hardly think any one would care to argue very long over so obvious and well-known a point.* Let us then see whether there is any evidence that butterflies can distinguish colours, or alternatively whether it can be shown that they are not blind to those portions of the spectrum which would probably be invisible to a totally colour-blind eye.

The only serious experiments with butterflies which I have been able to find are those of Seitz, recorded in a paper read by him at the International Congress of Entomology at Oxford in 1912. He observed that at El Kantara in Algeria the top of a certain range of hills was frequented by a yellow black-margined butterfly (*Anthocaris charlonia*), and was a meeting-place for the males who came there to mate. He made coloured paper models of the butterflies, and these attracted the real ones to such an extent that as many as six were seen at one time trying to pair with the paper model. They did not appear to see it at a distance of more than eight feet. To test the accuracy of their vision a graduated series of models was made differing in size, colour, and markings. Exact models were very attractive, whilst those which were of the right colour and markings, but three times the size, attracted the real males only for an instant. Accurately coloured models were always first visited, whilst those of similar but not of exactly matching colours were only noticed after the correct ones had proved disappointing. Models distinctly wrongly coloured were disregarded. The sense of smell was shown in these cases to have little apparent influence. From the position adopted by the male relatively to the female it was found that the male could recognise the head from the tail of the model only at a distance of about two to four inches, whilst the wrong colour seemed to be recognised at six feet, and abnormal size at from 1½ to 4½ feet.

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* See Poulton, "Colours of Animals," 1890, pp. 12–14.

From their behaviour in trying to pair with paper models fluttering in the wind, it was evident that the difference of texture between the paper and the real wing was not recognised.

As some evidence of colour perception Seitz remarks that the vertebrate eye can see red further away than blue. He observed in South America certain Pierine butterflies flying at some height over a mass of blue flowering shrubs, amongst which there were isolated flowers of a brilliant red. The butterflies precipitated themselves on the red flowers first, afterwards visiting the blue ones. This was the more remarkable as the blue-flowered plant was the food plant of the larva and might have been supposed to attract the insects first.

I have not quoted these observations because they carry us very much further, but they seem to be the only experiments of the kind so far recorded.

My own researches have not gone so far as I could wish. Much that was done in 1917 suggested other lines of investigation by which I hoped to profit in 1918. I had special flower-beds planted and other preparations made, only to be disappointed by the total disappearance of all butterflies at the end of August. The absence of *V. urticae* was especially noticeable, since in the garden where I had arranged my flowers this species usually flies in great numbers well into October.

However, while not claiming the essential virtue of being a "scientific chromatologist," I may give my results so far as they go, and leave others to judge of the extent to which they throw light on the subject.

It having been suggested that butterflies are either "short" in the red, or, if totally colour-blind, then red-blind, I endeavoured to prove or disprove this theory in the following way. I obtained a dye which I ascertained, by means of the spectroscope, transmitted only red rays. I am unable to give its composition, as it is a proprietary colour used for painting lantern slides. With this I painted over the eyes of numerous examples of *urticae*. I was very careful by microscopical examination to see that this was thoroughly done and that no pinhole of normal light could reach the eye. All the butterflies were marked so that they could be easily recognised again. That the insects so treated were certainly not totally blind, as they would have been had they been red-blind, was very completely shown by the fact that they immediately, or at least after a short period of "shock," flew to the window of the room, and also in some cases alighted on the curtains, the latter performance necessitating a judgment of distance little if anything removed from the normal. All my butterflies were then liberated, and both on that and succeeding days I observed them flying in the garden and alighting on flowers. Unfortunately I had not a sufficiently large number to judge fairly the extent to which their selection of flowers was modified by their "red spectacles." One I caught two days later was found on examination to have its coating of red quite unimpaired. The behaviour of these insects was in marked contrast to that of one whose eyes I covered with black dye. This totally blinded example, though repeatedly thrown into the air, merely fell to the ground and remained motionless, except for a certain amount of aimless creeping about. It would appear that *Ganoris brassicae*, *Pieris napi*, and *P. rapae* are distinctly shorter in the red than *V. urticae*, for similar treatment had a different effect. They still flew to a window, showing that a degree of light perception remained, but on being liberated flew aimlessly, and with marked lack of control.

It may be suggested that the examples of *urticae* which found the flowers in spite of their eyes being red, did so by the sense of smell. That this sense has little to do with their feeding habits I was easily able to show by coating the antennae of several specimens with shellac varnish. These continued to find the flowers with the same facility as before. In my view a strong scent may, and doubtless often does, help to attract butterflies, as, for instance, in the case of the well-known *Buddleia* flowers. I believe, however, that having once discovered a source of food, butterflies will return to it day after day, guided in great measure by the same remarkable locality sense, which in a much higher development has been so frequently observed

	Deep pink phlox.	White phlox.	Pale pink aster.	Pale mauve aster.	*Rudbeckia.* (Yellow, black centre.)	Deep purple aster.	Deep pink aster.	Pale mauve pansy.	Scarlet gladiolus.	Crimson lobelia.	White pink-eyed phlox.	Bronze Daisy. (*Helenium.*)	Purple stock.	Orange Montbretia.	Magenta phlox.	Pale mauve Michaelmas daisy.	Pale pink phlox.	Blue lobelia.	White aster.	Pink antirrhinum.
megaera			7		1	2	2				1	2		1		5				
io			5	2	9	3						3	3		2	1	3	1		
urticae	7	2	67	40	68	69	11	2			2	11	10		18	17	4		1	2
brassicae . . .			2									1	1				4			
icarus					1							2					1			
phlaeas . . .				1	2							2				1	1			
atalanta . . .					1							1			2	1				
egeria			1	1		2														
rapae				1													2	1		
pamphilus . . .			2																1	
c-album . . .			1			1														1
	7	2	85	45	82	77	13	2			3	22	14	1	22	25	15	2	2	3

in bees. My next experiments had to do with visits to flowers. A large herbaceous border formed a convenient observation ground, and I sought to discover whether any particular colour was more frequently visited than the rest. If butterflies are at first guided merely by the luminosity of the flower we should expect white to receive at least a fair share of attention. My observation showed that the disregard of white was most marked. In the border were several phloxes. The white phlox gained two visits only against forty-eight visits to the coloured ones. Of the latter the white pink-eyed phlox gained the fewest, and the magenta, nearest to purple, the most. The accompanying table shows the results of some 420 observations. It should be noted that no case was included where a butterfly merely jumped from one flower to another; I only counted those observations where the insect in full flight selected and alighted on a particular flower. From time to time I drove them away and then waited for their return.

I regret I did not make any careful calculation of the relative proportions of the various flowers, but it is certain that the asters were much less numerous than the others and there were but few Rudbeckias.

The failure of white as a conspicuous colour is due, in the opinion of my friend Dr. Church, to the fact that so much white light is reflected from shiny leaves and similar objects. One feature of the table is remarkable, viz. the total failure of scarlet and crimson. It is true that neither crimson lobelia nor scarlet gladiolus, from the situation of the nectary, is well adapted to butterflies, and experience, acquired or hereditary, might be considered to account for their disregard of these flowers. A large bed of scarlet pelargonium in the same garden was hardly ever visited by a butterfly, except occasionally by *egeria*, but probably this flower secretes very little nectar. As already suggested, butterflies are probably "red short," and this condition apparently varies in different species. I have shown that *urticae* is not by any means red-blind, while the Pierine butterflies experimented with seemed largely so. As to *egeria*, I have observed an example stop and examine with care every one of three or four scarlet petals which had been scattered on a lawn, though this does not prove that the insect could distinguish red except by a difference in the luminosity.

The *Rudbeckia* which proved so attractive is a bright yellow Composite with a nearly black centre, and one of the most conspicuous flowers in the border. In connection with this flower I discovered a very remarkable fact. Forel, in remarking that insects are rarely deceived by artificial flowers, suggests that what appear to be close imitations to us have a different appearance to the insect's eye, and colours which we should match appear different to them. I investigated this point by means of photography, and whilst artificial roses, violets, etc., all affected a photographic plate in the same way as the real flowers, the *Rudbeckia* gave an entirely different appearance in a non-screened photograph to that which it presents to our eye.

In the unscreened photograph only the tips of the petals are luminous, the rest being almost as black as the centre. I found no other flower presenting a similar peculiarity, and the observation is merely of value in connection with the appended table as suggesting that the flower appears as conspicuous to the butterflies as it does to us, and that their sight is of a similar nature. With the exception of the crimson and the white, the flowers most visited, according to my observation, were those which were most conspicuous to our eyes.

I now turned my attention to a large bed of asters, the colours of which were white, three shades of pink, and three shades of purple. Leaving the white out of consideration, for reasons already stated, it may be remarked that the purple flowers were particularly conspicuous and sharply defined on their green background, a fact due not, of course, to their luminosity but to their colour. I observed the choice of colour in 427 instances, and these were divided as follows :—

White	47
Pink	135
Purple	245

It should be noted that the pink flowers were more numerous than the purple in the proportion of about four to three. The butterflies were mostly *V. urticae*, but *io*, *atalanta*, and *C.-album* were also occasional visitors.

On the assumption that the preference for purple is due to the fact that this colour is more *conspicuous* and that the purple flowers are more apt to "catch the eye" of the insect, I proceeded to endeavour to analyse the conspicuousness of this colour. I first photographed three white, three pink, and three purple asters, using a screen which gave the effect of relative luminosity only. Photograph A, Pl. V gives the result which shows that the purple flowers were certainly not specially conspicuous on account of their luminosity. By using a set of spectroscopically tested screens I was then able to secure photographs representing the relative luminosities of the flowers when certain rays were eliminated. Thus in photograph B all the light rays except the yellow-green were eliminated, and the plate was therefore red and blue blind. In C only the red and part of the green rays were used, the plate being thus blind to blue and blue-green. In D all the rays except red were used, the plate being thus blind to red. I leave it to the reader to judge whether an eye, blind to any of the selected parts of the spectrum, would be likely to see the purple asters better than one which had a normal range. So far as luminosity is concerned, the purple flowers are less conspicuous in all the abnormally produced photographs than in that which gives the value with all the rays in use.

I consider it a fair assumption, therefore, that if the preference for the purple flowers is due to the greater ease with which they can be seen, the cause lies in the same property which makes them conspicuous to my own eyes, viz. the colour.

Before leaving the subject of flowers I may mention a few isolated observations which seem to have a bearing on the issue. An *urticae* picked out and dived at with great accuracy, from a distance of about four feet, a purple aster which lay between two scarlet flowers. Occasionally an example would settle—though not approaching from any distance—on the disc of an aster from which I had removed the ray florets. On the other hand, the yellow disc is not the guiding attraction, since they frequently flew to and settled on an aster bud which showed no yellow disc, and was only distinguished from the rest of the foliage by the coloured tips of the ray florets. On another occasion I observed an *urticae* pick out with certainty a very small yellow flower on the lawn, the latter being itself greenish yellow, and after tasting the flower it flew to and inspected a bit of yellow leaf lying some little distance away. Again I observed *P. rapae* flying over the lawn and picking out with precision some scattered and very minute yellow flowers whose colour was the only feature which appeared to distinguish them from their surroundings. Every one knows how our white

Pierine butterflies, when passing each other sufficiently closely, turn aside and carry on a flirtation in the air. This is sight and not scent, since different species will behave thus until closer proximity reveals the error. I observed a male *G. rhamni* fluttering over a pansy bed. Except for its well-known pale yellow colour it would have passed at a distance for *P. brassicae*. That species and also *P. rapae* were flying about over the pansies, and whenever they came within each other's visual field the usual flirtation ensued. But though *rhamni* and the other Pierines frequently came so near together as to be almost touching, neither took any notice of the other. This is the more remarkable since the female *rhamni* is nearly white, though it must be remembered that the pairing instinct probably does not develop in this species till the spring. But even supposing the *rhamni* was all intent on feeding, the *brassicae* certainly were not, and under the circumstances it is difficult to conceive any factor other than colour which caused them to ignore the *rhamni*.

In the early part of 1918 I arranged to carry out some experiments with *B. euphrosyne*, which is common in woods near Oxford. For this purpose I made paper models of the butterfly by cutting out photographs and colouring them. Of these I had two green, two blue, two crimson, two tawny yellow (the natural colour), two brown, and two clear pale yellow. In all cases the spots were black as in the real fritillary. In addition to the models I had a few real butterflies, long dead and dried.

In the first place the superior attraction of the real butterflies was very noticeable. The live fritillaries dipped at and examined the paper models, but in the case of the real ones they fluttered over them, touched them, and made every effort to obtain some response. As to the paper models, those of the natural colour attracted 27 individuals, red models attracted 18, and pale yellow 2. The other colours were not noticed at all. Note that the only colours other than the natural shade which attracted the live butterflies were those which might have been confounded with the real colour. So far as luminosity is concerned, the brown models (a rather pale brown) about equalled the naturally coloured models, whilst the red, though suggestive of the natural colour, had much less luminosity.

While pinning up my models I broke one of the real ones and threw away the fragments. This accident provided one of the most convincing incidents of the afternoon's work. I had the advantage on that occasion of the assistance of Mr. A. H. Hamm, who twice noticed a passing *euphrosyne* dipping to the ground and examining something in the grass and debris. On going to the place we found one of the wings of the specimen I had broken. Considering the innumerable small objects of similar *luminosity* which must have been lying about, I confess I am unable to understand what sense except that of colour could have guided the butterflies in these two instances. There is only one alternative, viz. scent. But the dead butterfly was many years old, and if it had any scent it was more likely to be naphthaline than anything else. But I was to receive a remarkable confirmation of this observation on my next visit to the wood. I again observed a *euphrosyne* hovering over something on the ground, and on going to investigate I discovered a large bud scale of exactly the golden brown colour of the butterfly itself. Truly this seems to me to be a remarkable performance for a "totally colour-blind" organism.

Having noted the superior attraction of the real butterfly over the paper model, a fact which I attribute to acuity of vision at close quarters, I prepared some models by bleaching real examples of the butterfly, dyeing them various colours and replacing the spots with black paint. Some of my "real" models were dyed golden brown like the normal insect, others were coloured red, blue, greenish yellow, and pale buff. Two of each were set up together with two untreated specimens. In half an hour there were 13 visits to the naturally coloured, 13 to the untreated, and none at all to the others. The only difference in the behaviour towards the dyed and the untreated examples was that the butterflies actually settled on the latter, but only hovered over the others, a proceeding again attributable to the slightly unnatural appearance, at close quarters, of the dyed specimens.

Later in the afternoon the butterflies seemed more intent on feeding than love-making, and the blue bugle flowers were, as usual, receiving the greater share of their attentions.

I set up one of each variety of my models. In this case there were five visits to the naturally coloured, and thirteen to the untreated. With one exception none of the other models was noticed. This exception was a blue model on which the *euphrosyne* actually settled. Its action was very characteristic; there was none of the excited flutter which always accompanies the usual amatory advances, but a direct alighting with precision. There can be no doubt that the insect had mistaken my blue model for a bit of the bugle flower, which it closely matched in colour.

One further experiment was made to test the apparent colour sense from the spectroscopic point of view. I discovered that the tawny yellow colour of the real butterfly contained many green rays, and also that the dye I had hitherto used was spectroscopically almost the same as the ground colour of the insect. I therefore sought some dye which would give me a visual colour resembling the real butterfly, but spectroscopically different. I found this in "Orange G," which when examined with a set of colour filters appeared to reflect no green at all, and certainly looked quite different to the colour of the real butterfly. I dyed a bleached *euphrosyne* with this and repeated my experiments. To an untreated model there were 38 visits; to one dyed with Orange G, 14. Allowing for the more natural appearance of the untreated specimen, the observation seems to show that the yellow which to my eye nearly matched the real butterfly, though spectroscopically a very different colour, was also a good imitation for the live insect.

On the same occasion I made a test to prove that scent, however lingering, is not a potent factor in guiding the butterfly, at least in the early stages of courtship. I put up a specimen of *B. selene*, a very similar butterfly of a different species, and it gained 15 visits.

In the course of these experiments I took occasion to observe the distance at which one butterfly appeared to become visually conscious of the presence of another, and I gained the impression that for this species the limit was about 3½ feet. The distance is greater when both insects are flying. If one is at rest another flying past has to come closer before it perceives it. A *euphrosyne* will pursue another species of butterfly on the wing if the other is more or less darkly coloured. It never notices any of our white Pierines.

I have stated that scent does not appear to be a strong factor in the early stages of courtship. It is quite otherwise when pairing is imminent or accomplished. Mr. Hamm noticed a pair of *euphrosyne*, *in coitu*, hidden on the underside of a small bush. We observed that every passing *euphrosyne* turned aside, even from positions whence the pair were invisible, and seeking them out, mobbed them furiously. Even after the pair had separated and flown away, other passing individuals turned aside and fluttered round the place. I have seen similar occurrences in connection with *C. pamphilus*, and I have recorded an example observed by Lamborn in a species of *Planema*. The remarks there made apply to the present cases.*

I have already explained my inability to continue these experiments during the past autumn. I hope to have better fortune in another season. So far, the chief results of my researches may be briefly summarised as follows:—

The peculiar refractive body at the base of the ommatidium in the butterfly eye, first observed in one species by Jonas, is commonly found in other species, and is a special structure of the trachaeal apparatus, varying in detail in the examples of different families investigated.

The periopticon in the butterfly eye seems to preserve in its structure the individuality and relative position of the nerve fibres relating to each facet.

There is every reason to suppose that the retinula cells are themselves the nerve endings of the receptive layer of the butterfly eye, and that the alleged existence of nerve fibres in or around the cone, or in the rhabdom, is an error due to incorrect observation. This view is strongly supported by the recent researches of Sanchez on the pupal eye.

The eucone eye, as found in butterflies, gives at the apex of each cone a small erect image made up of parallel rays which, proceeding down the rhabdom, stimulate the retinulae. The whole field of view is reproduced in a mosaic of correctly correlated elements forming a continuous and complete whole, the definition of which, owing to the comparative paucity of retinal elements decreases rapidly as the distance of the object increases, though at short distances the sight is comparatively acute.

The behaviour of butterflies under certain observed conditions lends strong support to the view that they can distinguish those differences of light-wave frequency which we call colour, and if the present evidence to that effect is not entirely conclusive, the testimony to the contrary is totally inadequate.

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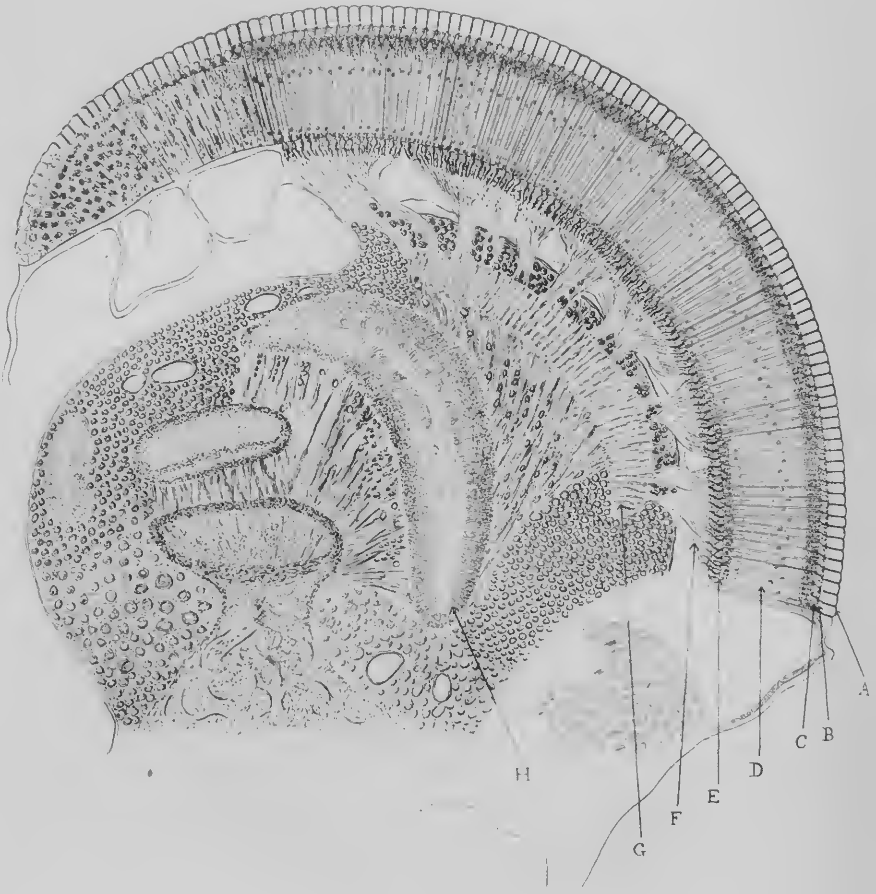
* See "Monograph of the genus *Acraea*," Trans. Ent. Soc., 1912, p. 8.

In the preparation of the foregoing work I desire to express my sincere thanks to Dr. F. A. Dixey, Mr. E. S. Goodrich, Mr. J. Bronté Gatenby, Mr. A. H. Hamm, Professor Poulton, Lord Rayleigh, Commander J. J. Walker, and others who have kindly helped me either with personal assistance or useful suggestions. Professor Poulton has specially helped me by kindly reading the proofs.

I have not given a bibliography of the subject, as the literature is so voluminous that it would occupy a great many pages of our Transactions, and economy of paper is still a necessity. Those specially interested will find bibliographies in nearly all the works I have mentioned in the text.



(H. Eltringham, del.)

(Oxford University Press.)

SECTION, EYE OF *VANESSA URTICAE.*

EXPLANATION OF PLATE I.

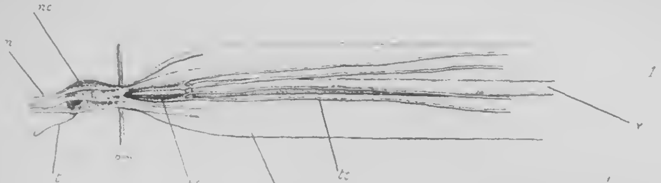
Section through an eye of *V. urticae* in the plane of the expanded wings × 60.

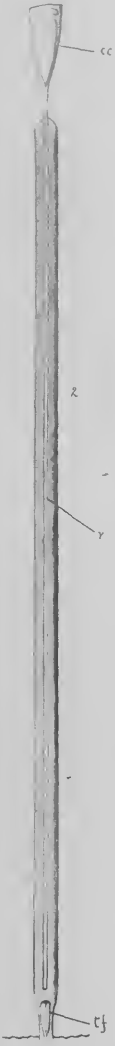
A. The corneal layer showing the lenses.
B. The *processus corneae.*
C. The layer of the "crystalline cones."
D. The ommatidia, each of which consists of eight elongated nerve end cells, the transparent inner longitudinal margins of which form the rhabdom.
E. The basal, or fenestrated membrane.
F. The nerve bundles leading from the ommatidia to the periopticon.
G. The periopticon.
H. The epiopticon.

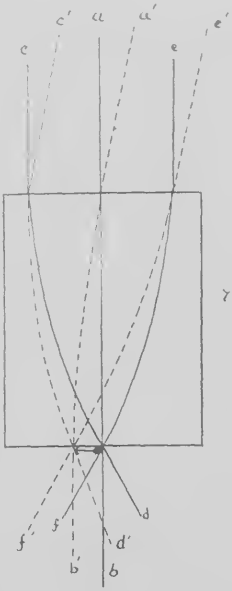
In the neighbourhood of the cones is seen a layer of pigment granules, the contents of the pigment cells there situated. A second less dense pigmentation occurs at the basal membrane. Just beneath the latter is a layer of heavily nucleated cells of which there is one to each ommatidium. The blank areas between the nerve bundles are tracheal spaces.

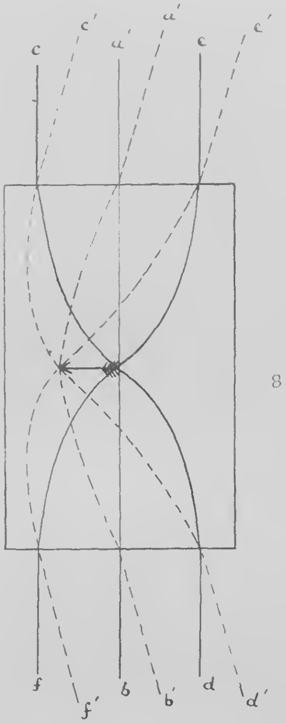
Explanation of Plate II.

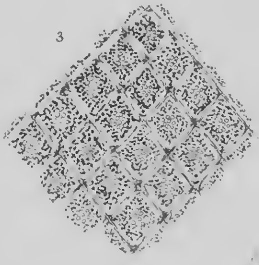
Fig. 1. Diagram of the proximal portion of an ommatidium × 1200.
    bm. Basal membrane.
    n. Nerve.
    nc. Nucleated nerve cell.
    t. Main tracheal tube.
    tt. Tracheal branches.
    ret. Retinula.
    r. Rhabdom.
    tf. Tracheal distributor.
2. An ommatidium and cone of *V. urticae* to show the relative size of the parts × 350.
    cc. Crystalline cone.
    r. Rhabdom.
    tf. Tracheal distributor.
3. Transverse section of periopticon showing regular arrangements of the nerve bundles × 1350.
4. Transverse section of nerve bundles, nucleated cells, and tracheae just below basal membrane × 1350.
    n. Nerves.
    t. Tracheal tube.
5. Transverse section of tracheal distributor × 1350.
    n. Nerves (retinulae).
    c. Cruciform chitinous body in distributor.
    ts. Tracheal spaces.
6. Transverse section of ommatidia above tracheal distributor × 1350.
    tt. Tracheal branches.
    r. Rhabdom.
    ret. Retinula.
7. Diagram of a lens cylinder of its own focal length.
8. Diagram of a lens cylinder of twice its own focal length.

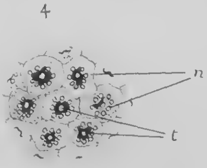


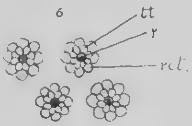


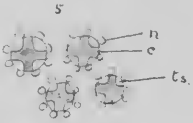












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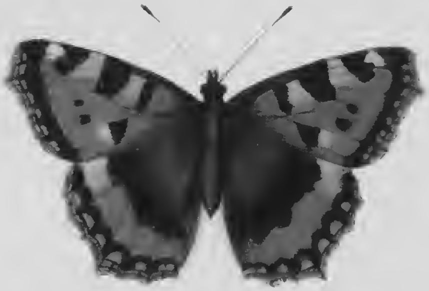
BUTTERFLY VISION.



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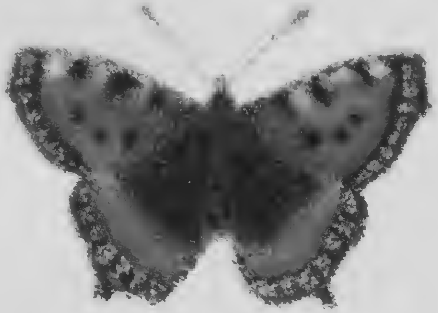

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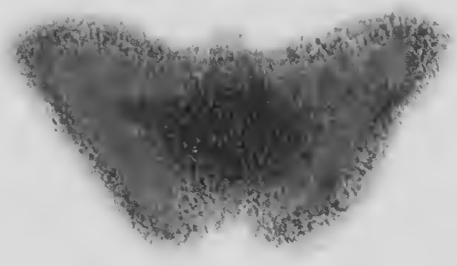

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H. Eltringham del. Sun Engraving Company Limited.

BUTTERFLY VISION.

EXPLANATION OF PLATE III.

FIG. 1. A Tortoiseshell butterfly as it appears to the human eye.

2. The same as it might be supposed to appear to another of the same species, at a distance of two inches, assuming the correctness of the original mosaic theory.

3. The same, on the same assumption, at a distance of twelve inches.

Note.—An image such as Fig. 3 may fairly be regarded as about the limit of recognisable visibility. It is produced by approximately 72 facets. Now the number of facets engaged varies inversely as the square of the distance, hence at three feet $\frac{1}{9}$ of 72, or eight facets only would be engaged. If, however, the theory here advanced be correct (*vide* p. 28), the image is eight times more distinct than was previously supposed, and hence at three feet the image would be equal to that produced, on the older theory, by 8 × 8, = 64 facets.

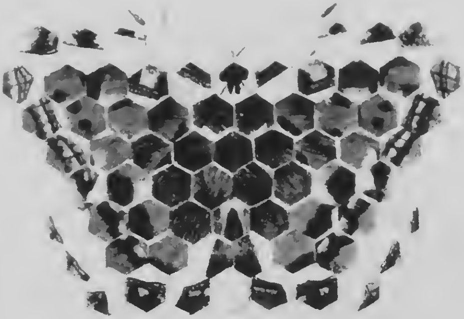
In other words, Fig. 3 would represent very nearly the degree of definition at a distance of three feet, and this distance is about the observed limit of recognition in these insects.

EXPLANATION OF PLATE IV.

FIG. 1. A Tortoiseshell butterfly as it might be supposed to appear to another of the same species, at a distance of twelve inches, on the assumption that each facet unit gives a definite but inverted image.

2. Photograph, taken with a 12 mm. objective, of the erect image in the eye of a glow-worm, *Lampyris noctiluca.*

The eye was mounted on a cover slip with a drop of dilute glycerine and a transparency of the portrait placed about two inches in front of it. The actual area of the image is about ·15 sq. mm. The definition is not nearly so good as when the image is viewed in the microscope by the human eye. Also it has lost much in reproduction.



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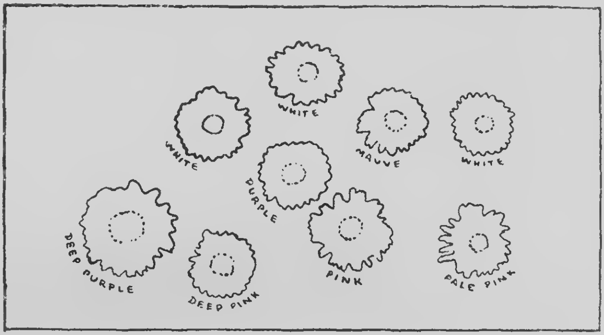
H. Eltringham, del et photo. (Oxford University Press.)

INSECT VISION.

EXPLANATION OF PLATE V.

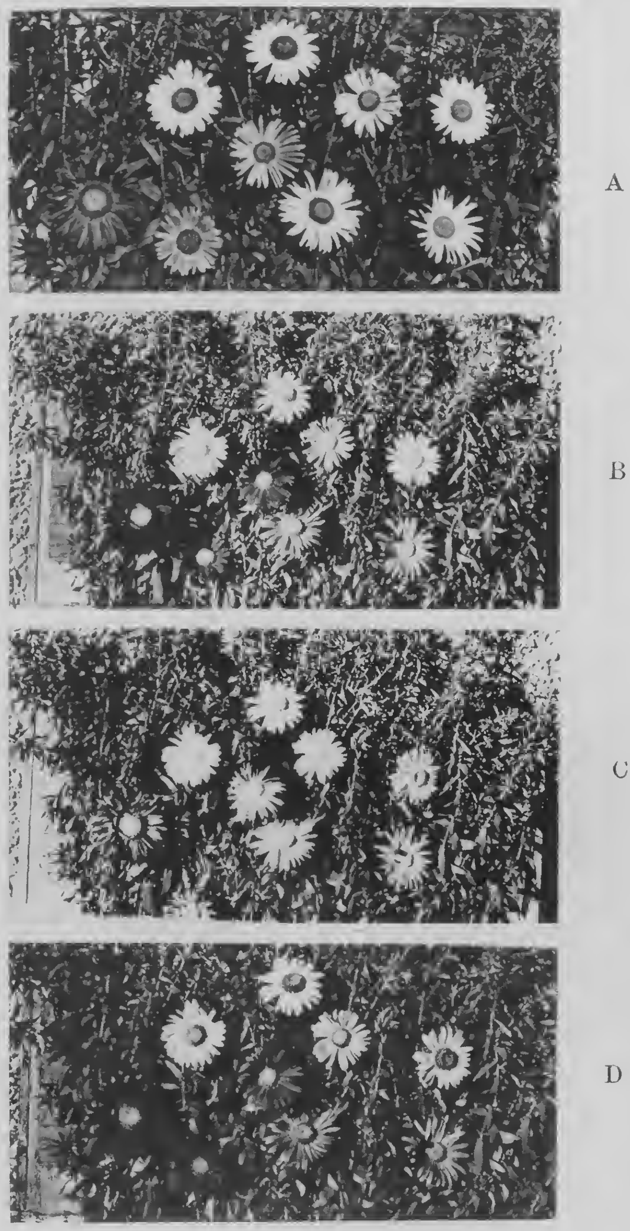


A. Photograph of asters so screened as to give the relative luminosity values.

B. Ditto when only yellow green rays are used, the plate being thus red-blue blind.

C. Ditto when red and part of green rays are used, plate blue-blind.

D. Ditto with red rays eliminated, plate red-blind.



H. Eltringham, photo. (Oxford University Press.)

PHOTOGRAPHIC COLOUR-VALUES OF FLOWERS.

FURTHER NOTES ON SCENTS IN BUTTERFLIES.

BY

G. B. LONGSTAFF, M.A., M.D., F.L.S., &c.

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During the two years that have elapsed since the appearance of my list* of the butterflies which have been observed to possess a scent, I have had further opportunities of investigating the subject.

Butterfly scents have been divided by Fritz Müller and Dixey into two categories:—

(1) Attractive scents: in the very large majority of cases confined to the male sex. These are almost always agreeable to the average human perception.

(2) Repulsive or protective scents: usually common to both sexes, and often strongest in the female. These are, for the most part, disagreeable to man, or even disgusting.

As perhaps might have been expected, further investigation, while extending the basis of facts upon which these generalizations have been made, has revealed more and more exceptions.

The exceptional occurrence of female butterflies with attractive scents needs further explanation. Moreover, my own experience with scents believed to be repulsive convinces me that if such scents are really protective they must be far more repulsive to the enemies of butterflies than they are to man. All lovers of dogs must have noticed that many odours which give pleasure to us excite disgust in them, and *vice versâ*.

In the following notes an asterisk indicates that the species is one that I have not previously dealt with.

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* "Butterfly Hunting in Many Lands." 1912. pp. 490–516. Full references to the authorities are there given. The species are dealt with here in the same order to facilitate comparison.

NYMPHALIDÆ.

ITHOMIINÆ.

* *Ceratinia fenestella*, Hew. (Trinidad, 1913). Out of three examined, a ♀ had an odour resembling musty tobacco. Fritz Müller detected a rather faint scent in *C. eupompe*, Hb.

* *Mechanitis lycidice*, Bates, and *M. veritabilis*, Btl. (Trinidad and Venezuela, 1913). Ten specimens of each of these closely allied species were examined. In one only, a ♂ of the first named, was a slight scent suspected in connection with the fringes. So far as it goes this confirms Fritz Müller's record of a very faint scent in the ♂ of *Mechanitis lysimnia*, F.

* *Eutresis hypereia*, Dbl. and H. (Venezuela, 1913). A ♀, the only specimen met with, gave out both during life and after death, a strong odour like that of cockroaches.

DANAINÆ.

Danaida archippus, F. (Dominica and Venezuela, 1913). 4 ♂♂ and 2 ♀♀ examined. Previous results confirmed, but in one ♀ the scent is described as "not strong, scarcely disagreeable."

Danaida eresimus, Cr. (Venezuela, 1913). Of 2 ♂♂ examined, one had a sweet scent, somewhat aromatic in character, the other a "not unpleasant" scent. In 1907 I was somewhat in doubt as to the ♂ possessing a scent.

* *Lycorea atergatis*, Dbl. (Trinidad and Venezuela, 1913). Six specimens were examined, 3 ♂♂, 3 ♀♀. All the ♂♂ had the tufts everted, but in only one of them could any scent be detected, it was slight and resembled that of a cockroach. One of the ♀♀ had a similar slight odour, in another the scent was compared to that of a cigar box. Fritz Müller found an extremely strong, rather disagreeable odour, in "*Lycorea* sp."

SATYRINÆ.

Pararge megæra, L. (Spain, 1913). In 4 ♂♂ out of 9, I succeeded in detecting a more or less distinct scent of chocolate, without the vanilla element.

* *Pararge mæra*, L. (Spain, 1913). I took but one specimen, ♀, which had a scent of pure chocolate, strong during life, less strong after death.

NYMPHALINÆ.

Didonis biblis, F. (Trinidad and Venezuela, 1913.) 4 specimens examined, 3 of them ♂ ♂. No scent was detected in any of them, so that in this species I have again failed to confirm Fritz Müller.

* *Byblia ilithyia*, Drury. (Sudan, 1912). A ♂ and 4 ♀ ♀ were examined: the former had a sweet aromatic scent, which struck me as like scented tobacco; of the latter, one had a similar scent, but less strong; another a scent compared to chocolate; a third to that of *Teracolus protomedia*, of which, later. This scent in the female tallies with earlier observations on *B. goetzius*, Herbst.

Hypolimnas misippus, L. (Sudan, 1912). In 2 ♂ ♂ I found no scent, but in 2 ♀ ♀ out of 4, I detected a slight treacly odour. Compare Dr. Dixey's observations (*op. cit.*, p. 502).

Victorina stelenes, L. (Trinidad, 1913). 2 ♂ ♂ were taken, one appeared to have a slight flowery scent; I was not very certain about this at the time, but find that it agrees with my earlier experience with this fine insect.

Agraulis vanillæ, L. (West Indies, 1913). Out of 4 ♂ ♂ examined, one had the stable-like odour noted in 1907.

Colænis julia, F. (West Indies, Trinidad, and Venezuela, 1913). 4 ♂ ♂ and 4 ♀ ♀ were examined; in the 4 ♂ ♂, and doubtfully in one of the ♀ ♀, a scent was noted, in only one instance strong, said to be "peculiar," "sweet," "like treacle," or "like ginger-bread nuts." These results are in concordance with my experience of the sub-species *cillene*, Cr., in Jamaica.

[I follow here the arrangement adopted in "Butterfly Hunting in Many Lands," but I am now disposed to consider *Agraulis* and *Colænis* as Heliconines.]

HELICONINÆ.

Eueides aliphera, Godt. (Trinidad and Venezuela, 1913). 4 ♂ ♂ and 3 ♀ ♀ examined. In one ♂ no scent was observed; the other three had both during life and after death an odour compared to rancid lamp-oil, or to acetylene, varying from very slight to strong. 2 ♀ ♀ had a similar scent to the ♂, but the third is noted as having "a sweet, pleasant scent." These results, speaking generally, confirm those previously obtained.

Heliconius hydarus, Hew. (Trinidad and Venezuela, 1913). Previous results were confirmed, but 2 ♂ ♂ and 1 ♀ *H. euryades*, Riff., gave negative results.

* *Heliconius ethilla*, Godt. (Trinidad, 1913). The only specimen at my disposal, a ♀, had a strong tobacco-like odour.

LYCÆNIDÆ.

**Thestor ballus*, F. (Spain, 1913). 8 ♂♂ were examined: all had a scent, not very strong, compared sometimes to chocolate, sometimes to "chocolate sweets" (*i.e.*, with a vanilla element). 4 ♀♀ appeared to be scentless.

PAPILIONIDÆ.

Pierinæ.

Catopsilia florella, F. (Sudan, 1912). The strong luscious scent of the ♂ was confirmed,

Rhabdodryas trite, L. (Dominica, 1913). The only specimen taken, ♂, yielded a "sweet pleasant scent; not so strong or luscious as *C. eubule*," confirming Fritz Müller.

Phœbis agarithe, Bsd. (St. Lucia, 1913). A pair had a "strong fetid butyric odour"; ? emitted by the ♀.

Callidryas eubule, L. (West Indies, Trinidad and Venezuela, 1913). The strong luscious scent of the ♂, compared by me to *Freesia* but by a friend to carnation, was amply confirmed, as was also the butyric odour of the ♀.

Gonepteryx rhamni, L., and *G. cleopatra*, L. (Spain, 1913). These butterflies were found flying together at Ronda, Andalusia, in March.

9 ♂ *cleopatra* were examined: in all a scent was found; in one it was described as "very slight," in another as "decided, but not very strong," in four as "strong"; in 8 out of the 9 it was unhesitatingly compared to that of *Freesia*.

8 ♂ *rhamni* were examined: in 5 I was unable to detect any trace of scent, either during life or after death, but in the other 3 the living insects had a very faint scent, which I could not clearly describe, but in each case noted that it was not that of *Freesia*.

These results are in complete accordance with those obtained in Algeria in March, 1905.

It would, however, appear that I paid little or no attention to the female *Gonepteryx* in Algeria, although I sent home four specimens, of which three may be referred to *cleopatra*, the fourth probably to *rhamni*.

But at Ronda I examined 9 ♀♀, all seemingly referable to *cleopatra*, and was not a little surprised to find a scent in all of them:

this scent was more distinct than that of the male *rhamni*, but much less strong than that of the male *cleopatra*. To me it was agreeable, sweet, and suggested *Freesia*.

Are we to regard *rhamni* and *cleopatra* as distinct species of which the females closely resemble one another? Or are we to look upon them as but one species with a (locally) dimorphic male?

Dr. Dixey gave to the Entomological Society some years ago an admirable summary of the facts, which was fully reported at the time.†

An obvious question arises: can the scent be directly connected, or indirectly correlated with the orange scales? Mr. Enock's record of ants attacking *G. rhamni* and confining their depredations to the orange spots is very suggestive, especially in the light of somewhat similar observations as to *Danainæ*.

**Aphrissa statira*, Cr. A ♂ had, when alive, a slight sweet scent.

Colias edusa, auct. (Spain, 1913). 6 ♂ ♂ were examined; in three I was unable to detect any odour, in two a very slight chocolate-like scent was suspected, in one I satisfied myself that a slight but distinct scent was present, which I was disposed to compare to that of clove-pink. I was, however, unable to localise the scent in the "patches."‡

Terias nise, Cr. (W. Indies, Trinidad, and Venezuela, 1913.) 19 ♂ ♂ were examined of which 5 had a sweet scent, compared in several instances to the peculiar smell of *Convolvulus arvensis*. 7 ♀ ♀ gave negative results. These observations confirm my experience in 1907, though the positive results are proportionately fewer.

Teracolus protomedia, Klug (Sudan, 1912)). In 6 ♂ ♂ out of 24 I detected a slight scent, not easy to describe; the words "dusty," "stuffy," "musky," "peculiar," "like wood," and "very faint *Freesia*" appear in my note book. Previous results were thus confirmed.

**T. eupompe*, Klug (Sudan, 1912). In two ♂ ♂ out of a large number examined a slight scent was observed, in one noted as "sweet," in the other as "stuffy."

T. halimede, Klug (Sudan, 1913). A ♂, one of many, had a distinct musky odour.

**T. pleione*, Klug (Sudan, 1913). A ♂, one of many, had a distinct musky odour.

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† Proc. Ent. Soc. Lond. 1905. pp. xxxvi—xli.

‡ See Dixey, Proc. Ent. Soc. Lond., Oct. 5th, 1904, p. lvii,

**T. evippe*, L. (Sudan, 1913). A ♂, out of 12 examined, yielded a scent like *Freesia*.

**T. evarne*, Klug (Sudan, 1912). Out of a large number of ♂ ♂ five were found to have a scent: it was distinct and sweet in character, in one compared to *Freesia*, but in another described as "somewhat medicinal."

Having captured large numbers of many species of *Teracolus*, I am forced to the conclusion that the scent of the males is either very slight, or very transient, or for some other reason more difficult to detect than scents in some other genera.

**Calopieris eulimene*, Klug (Sudan, 1912). 3 ♂ ♂ out of 21 appeared to have a faint sweet scent, once suggesting gorse.

**Leuceronia buquetii*, Bsd. (Sudan, 1912). Out of 4 ♂ ♂, I suspected a faint sweet scent in one, and noted a "slight, scarcely agreeable" scent in another.

**Euchloë bellidice*, Hübn. (Spain, 1913). Out of 19 ♂ ♂ examined a scent was detected in 15; this was variously estimated as "very slight," "slight," "distinct," or "decided"; in most cases it was described as "sweet," once compared to that of *Freesia*, once said to be "somewhat aromatic," another time "scarcely pleasant." Only 3 ♀ ♀ were examined; one had an unpleasant odour, the other two were scentless. [This is *A. belia*, Cr.].

This species flies with the next, but is commoner and more generally distributed, and a larger insect.

**Euchloë tagis*, Hübn. (Spain, 1913). Of this local species I examined 13 ♂ ♂, 5 ♀ ♀, and one of which the sex is uncertain. In none of them was any odour detected.

The two preceding species are closely allied, so that exceptional specimens of the former are said to resemble the latter. It is interesting to find that they differ in the matter of scent production.

**Euchloë belemia*, Esp. (Spain, 1913). 15 ♂ ♂ were examined: two had a "pleasant scent," which was "slight" in one, "very slight" in the other. In six others a scent was suspected, in one of which it appeared to be "very sweet." 11 ♀ ♀ gave negative results. This butterfly flies swiftly.

Daptonoura lycimnia, Cr. (Trinidad and Venezuela, 1913). Of 11 ♂ ♂, one appeared to be scentless, the other 10 all had a decided sweet luscious scent, compared to that of *Freesia*. My experience in 1907 was thus fully confirmed, but my results are not in complete accordance with those of Fritz Müller, who found the scent of the ♂, though very delicious, rather faint and often hardly distinguishable. Two ♀ ♀ were examined but no scent found. (Compare *op. cit.*, p. 511).

Belenois gidica, Godt. (Sudan, 1912). Of 13 ♂ ♂ all appeared to be scentless, but in 1 ♀ out of 5 a faint scent was detected.

Belenois mesentina, Cr. (Sudan, 1912). I found the ♂ to have a slight scent, variously suggesting the adjectives "musky," "aromatic," "flowery." Previous results were thus confirmed.

Pieris (Perrhybris) calydonia, Bsd. (Venezuela, 1913). 11 specimens, all ♂, were examined; in 4 of these there was a distinct scent, described as "flowery" or "like *Freesia*"; in two a somewhat unpleasant scent, suggesting pomade, was found. On the whole previous results were confirmed.

**Pieris (Perrhybris) sevata*, Feld. (Venezuela, 1913). 2 ♂ ♂ had a slight but distinct flowery scent; 2 ♀ ♀ were scentless.

**Pieris (Perrhybris) phileta*, F. (W. Indies and Venezuela, 1913). Out of 10 ♂ ♂ examined, only four yielded a scent, twice doubtfully described as "peculiar," once as "heavy, somewhat unpleasant," once as "strongly fetid." Of two ♀ ♀ one had a "slight fetid odour." In 1907 I failed to detect any odour in this species.

**Synchloë glauconome*, Klug (Sudan, 1912). 3 ♂ ♂ out of 8 yielded a distinct sweet scent like that of *Freesia*.

**Synchloë daplidice*, L. (Spain, 1913). Of 32 ♂ ♂ examined, 24 had a scent. This was in no case strong, but variously estimated as "very slight," "slight," "distinct," or "decided"; it was variously described as "aromatic," "like sweet-briar," or "scarcely pleasant," but more often as "sweet," and in a majority of specimens was compared to that of *Freesia*. Of one of the 24 ♂ ♂ the note says that observation in the field showed "a slight sweet scent," but that at home the butterfly was found alive in its envelope, and emitted "a strong scent, somewhat like that of *P. rapæ*." One observation gave a doubtful, seven gave negative results. In 8 out of 10 ♀ ♀ examined, no scent was detected; in one "a very slight but very sweet scent" was noted; of another it is recorded "a very slight *Freesia* scent: no doubt about it."

PAPILIONINÆ.

**Thais rumina*, L. (Spain, 1913). In 10 out of 11 ♂ ♂, and in all the 7 ♀ ♀ examined, a scent was easily detected, though sometimes it was but slight; it appeared to be alike in both sexes. From time to time I have attempted to describe this scent by such words as "somewhat unpleasant," "disagreeable," "? like rue," "peculiar," "musty," or "somewhat like musty straw, but less disagreeable."

When examining the specimens at Oxford in July, 1913, five months after capture, and again in October, eight months after capture, the scent was still very distinct, even in the presence of naphthalin. Mr. Bagnall thought it "musky," Mr. Hamm "musty," Dr. Carpenter thought it "like smell of pepper, but mild pepper," while Dr. Dixey suggested "the smell of the pepper-tree." The last comparison struck me as apt.

T. rumina has a striking pattern, similar on both upper and undersides, it is slow in its movements and bold in its behaviour; further it is hard to kill; when it is added that both sexes have a peculiar scent, it will be seen that it has all the characteristics of a protected species.

**Papilio cymochles*, Dbl. (Trinidad, 1913). A ♂ had a somewhat unpleasant odour, described as "stuffy"; a ♀ a scent described as "like that of an old pipe."

**Papilio machaon*, L. (Spain, 1913). Two ♂ ♂ had a strong disagreeable odour of musty straw.

**Papilio podalirius*, L. (Spain, 1913). A ♀ had a decided odour like straw, but not disagreeable.

Yet once more I appeal to field naturalists to join in the investigations of these interesting perfumes, which hitherto have attracted the attention of so few.

Highlands, Putney Heath:
October 24th, 1913.

XV. *On the Histology of the Scent-organs in the Genus* Hydroptila, *Dal.* By H. ELTRINGHAM, M.A., D.Sc., F.Z.S.

[Read November 5th, 1919.]

PLATE XXII.

MY friend Mr. Martin E. Mosely has made a discovery of the first importance, which should prove of the greatest interest to entomologists. In a paper read before this Society on October 15th (p. 393), he described the external features of certain organs in the heads of various species of the Trichopterid genus *Hydroptila*.

Mistrusting his own skill as a microtomist with a lack of faith which, judging from some of his excellent preparations, I regard as unfounded, he has done me the honour to hand over to me a supply of material for the investigation of the minute structure of these organs. Just as Science generally is indebted to him for his discovery, I am personally under an obligation to him for enabling me to carry out an examination of unusual interest and fascination.

Some time ago I described and illustrated the scent-organs in certain male Danaine butterflies (Trans. Ent. Soc., 1913, p. 399; 1914, p. 152).

It will be remembered that these included certain eversible brushes located in the extremity of the abdomen. These brushes were formed of hairs of varying structure set on the inner surface of an eversible membranous bag, so that when the latter was everted, doubtless by fluid pressure, the hairs projected from its now outer surface. In some cases the scent material was obtained from glands in the wings, whilst in others the brushes themselves exhibited a glandular structure.

We know from the work of Dr. F. A. Dixey and others that certain special scales on the wings of butterflies act as scent-organs. In all these cases the scent-scales, brushes, glands, etc., are of comparatively considerable size, and occur on insects which, even in the case of Lycaenids, are large compared with *Hydroptila*. These little creatures are themselves no larger than the brush of a Danaine butterfly, yet, as Mr. Mosely has shown, they possess eversible brushes, scent-scales, expanding membranes and tubercles, of a high degree of complication. Moreover, the organs in question are not located in the abdominal extremity, but in the back of the head.

It is a most interesting case of what may be termed the independent development of practically homologous structures in insects of different orders, since, however nearly related the Lepidoptera and Trichoptera may be, it cannot be urged that these scent-organs in the two orders had a common origin.

On Descriptive Terms.

Before describing the organs it may be well to define the terms applied to some of the structural details.

It has been suggested to me on more than one occasion that the term *hair* should be confined to mammalian hairs, and that insect hairs should be known by some other word. I referred to this matter in a note to my paper on the Danaine scent-organs (*l.c.*), and I am still unable to see the necessity for any alteration in terms.

The Oxford Dictionary defines a hair as " One of the cylindrical filaments that grow from the skin or integument of *animals*, especially of most mammals . . . ; applied also to similar looking filamentous outgrowths from the bodies of insects and other invertebrates, *although* these are generally of different structure."

Similarly, we speak of the *scales* on the wings of Lepidoptera and on other insects, without in any way implying that they are of the same nature as the homonymous structures in fish.

There is a greater difficulty which would not be removed by the invention of another word for insect hairs, namely, that of deciding the precise point at which an insect hair becomes an insect scale. Under a low power a Trichopterous insect such as *Hydroptila* may be regarded as covered with hairs on wings and body, but on examination with a higher magnification it is seen that the structures in question would be better described as elongated scales. Furthermore, we have in insects certain growths known as scent-scales or *androconia*. It is an unsatisfactory term, but as its signification is generally understood we may retain it for the present. Is this term to be applied to any modification of insect scales or hairs characteristic of the male insect, or is it to be confined to those structures that have a direct connection with glandular tissue of a sexual character? If the former, the word becomes almost too vague to be useful, if the latter, then the brush hairs in *Hestia* are androconia, whilst those in *D. chrysippus* are not, and so before we can use the term at all, we must have a knowledge of the histology and perhaps even of the embryology of the structures to which we refer.

It would seem, then, that if we aim at greater precision in terms we merely arrive at the position of a person who cannot describe a landscape because he has not measured the elevations to see whether they are hills or mountains, and fears to mention a wood till he has identified the species of trees it contains.

In describing the organs in these small Trichoptera I propose, then, to use the word hairs when referring to the long, fine bristles which form brushes similar in form to the brushes described in the *Danainae*. In several species there are structures which, though of varying form, resemble more or less closely the scent-scales already known to occur in many Lepidoptera. Though the word is unsatisfactory I shall refer to them as androconia, for the reason already stated.

Finally, there are the elongated scales or hairs found so plentifully on the wings and body. As the order is known as "hairy winged" as distinguished from "scale winged" we will call them the cuticle hairs.

The organs to be described are, of course, only found in the male sex.

Descriptive.

Hydroptila sparsa Curtis.

Four eversible tubercles arise from a membrane lying across the back of the head, such tissue forming the lightest possible protection for the brain situated immediately beneath it. Towards the upper and anterior edge of this membrane there is on its underside a layer of moderately large cells which may be merely hypodermal, but probably also have a glandular function. Arising from this membrane on its upper portion and on either side of the centre line is found a small tuft of very remarkable androconia

(Plate XXII, figs. 1 and 2). They are pyriform with long delicate stalks, and the outer expanded portion is clothed with filaments apparently similar to those in the scent-scales of certain Pierine butterflies. Apart from their shape and position they possess a feature which I have been unable to find in any other species examined. Each has beneath its socket a large, granular, heavily nucleated cell, distinguishable by its size and structure from the other cells of the layer in which it lies. There are some twelve of these androconia on each side of the centre line. There is no trace of hairs or brushes. Structures somewhat resembling the "brush bags" in other species are present, but without hairs. These are the four eversible tubercles already referred to. There are two of these on each side, and when fully expanded they extend to a considerable length, as may be seen on reference to Mr. Mosely's photographs. The material of these tubercles is an extremely delicate chitin, not of the same nature throughout its entire length, since the proximal portion takes a different stain from that of the remainder.

A section through the partly everted tubercle (fig. 3) shows a few scattered cells on the inner side. These are probably hypodermal cells which have been displaced in the process of preparation. The whole tissue of the tubercle when not fully extended is thrown into a multiplicity of interlocking folds. When retracted it is inverted and not merely collapsed, and this remark applies to those eversible tubercles in other species, which are lined with hairs and form brush bags. A similar inversion takes place in the brush bags of the Danaine butterflies, but it can there be accounted for by the presence of a muscle attached to the apex of the bag, and acting as a retractor when the fluid pressure is released. It is a remarkable fact that no such muscle can be found in any of the species of *Hydroptila*. This is not due to any fault of the preparation. Muscle tissue is amongst the easiest of all to recognise in insect sections, and in my preparations other tiny muscles inside the head are easily observable.

So far I am unable to account for the inversion of the retracted tubercle, unless it is to be explained by some complicated condition of a variable coefficient of elasticity in different parts of the membrane. The fact of its differential staining already alluded to does not help us, as this occurs only in the present species.

The lobes which cover the eversible tubercles when retracted are somewhat of the shape and appearance of half an almond shell, but much thickened towards the base. Owing to the peculiar angle of view in fig. 1 their shape is not well shown. On the outer surface of the lobes the chitin is perforated by a multiplicity of openings, and in ordinary preserved material some of these perforations emit cuticle hairs of considerable length, whose stalks are deeply embedded in the hypodermal epithelium within. This epithelium may possibly be glandular, since it presents an active appearance (fig. 5). Mr. Mosely informs me that the lobes in this and some other species are densely covered with these cuticle hairs when the specimen is in fresh condition, but that they become detached with great facility, so that the lobes, even in life, are often found practically naked. We may therefore assume that in fresh examples each perforation carries a cuticle hair. We may further venture to speculate as to whether when detached they may not conceivably act in a manner analogous to that of the "dust particles" which are so marked a feature in some of the butterflies already referred to, and of which the use has, since their discovery, been actually observed and recorded by Carpenter (Proc. Ent. Soc., 1914, p. cxi).

Plate XXII, fig. 1 shows the head of this species with the lobes turned back and the tubercles in a condition of partial eversion. Fig. 2 shows two of the androconia with their special cells. Fig. 3 a highly magnified view of one of the tubercles partly everted. Fig. 4 a section through one of the lobes. Fig. 5 part of the same more highly magnified to show the cells lining the outer cuticle. Fig. 6 a vertical longitudinal section through the head and one of the tubercles incompletely everted.

H. simulans Mosely.

Each lobe in this species may be said to resemble externally half an acorn. The basal portion is thick and well rounded, and shows the same perforate structure as in *H. sparsa*. The upper part is smooth and rounded and of a somewhat darker colour, whilst the apical part is thin, flat, and subtriangular. On its inner surface each lobe has a deep oval concavity forming a receptacle for the retracted brush. No sign of androconia has been detected in this species, but the surface of the concavity of the lobe has a peculiar structure as though formed of minute chitinous plates, giving it somewhat the appearance of a tessellated pavement. The thicker basal portion of the lobe shows in section a lining of hypodermal cells probably of a glandular nature. Beneath the lobes and directed upwards and centrally are two brushes formed of a mass of golden yellow hairs arising from small sockets in the lining of a brush bag, the whole presenting an arrangement and appearance closely resembling that in many Danaine butterflies. A section through the head in the plane of the long axes of the two brushes is shown at fig. 8. From this it will be seen that the hairs arise over nearly the whole length of the bag, and hence when the latter is everted the appearance is somewhat that of a test-tube brush or pipe cleaner. The hairs are slightly thickened towards their distal extremities. In the substance of the bag are two distinct layers, the inner one being thin chitin thrown into a multiplicity of folds and bearing the sockets of the hairs. These sockets are of peculiar formation, and resemble the structures known to botanists as bracts. Outside this membranous layer is a glandular epithelium consisting of granulated and heavily nucleated cells shown in fig. 10.

The hairs themselves are not smooth, but have an elaborate structure which I have endeavoured to represent in fig. 9. There are whorls of laminate projections having irregularly curved distal margins. Also the projections are not continuous round the hair, but the rings are intercepted at irregular intervals by more or less vertical fissures. The elaborate structure of the minute brush hairs in this and other species is one of the most notable features of the scent-organs.

The general arrangement in *H. simulans* seems to be analogous to that in the butterflies *Trepsichrois mulciber* and *Hestia lynceus*, in which the brush hairs themselves are the direct vehicles of a secretion produced by glands at the bases of their sockets. Fig. 7 is a view of the head with the lobes closed.

H. forcipata Eaton.

In this species the lobes are very small as is the whole area of the scent-organs. Fig. 15 is a view of the posterior surface of the head with the lobes turned back. Here we find a new modification in the fact that the lobes are provided on their inner surface with a membrane which can be distended, probably by fluid pressure. On this membrane are a few androconia of not quite circular section, having long stalks and a very deeply ribbed surface. The androconia are probably porous or very absorbent, as they stain rapidly and intensely. The outer surface of the lobe is covered with extremely minute black setae having widened bases, like rose thorns. A section through the lobe, fig. 19, shows that the extensible membrane contains at its base a mass of granular, heavily nucleated cells which doubtless furnish a volatile secretion. The androconia are not provided in this species with special cells at the bases of their sockets. Indeed, this is a condition I have found only in those of *H. sparsa*. Fig. 16 shows a highly magnified view of the inner face of one of the lobes. The lobe itself is seen to the left, whilst the membrane extends all over it and some distance to the right. The androconia lie on, and arise from, the membrane in an irregular fashion. The small bunch of hairs here shown does not in reality arise from the membrane of the lobe, but from that on the back of the head between and beneath the lobes, though in this dissection they have come away with the lobe itself. They take the form of a mere tuft of bristles, and though the membrane from which they arise may be slightly extensible there is no eversible bag. The hairs are of the complicated structure shown in fig. 17 and in transverse section at fig. 18. There is a very slight development of glandular epithelium at the origin of these hairs. They have a very thin cuticle, and in section show a very large lumen.

H. maclachlani Klap.

The structure in this species bears a close general resemblance to that in *H. forcipata*. The lobes are smaller and very inconspicuous, but their extensible membranes seem to be more highly developed. Fig. 23 shows a section through one of the lobes and the neighbouring structures. The membrane has a dense mass of glandular tissue at its base, and bears a number of androconia, one of which is represented at fig. 20. These are very deeply ribbed and circular in section. On one lobe I have mounted there are twenty-one, and on another eighteen. The little pencil of hairs is as in *H. forcipata*, but the hairs themselves appear to be longitudinally striated and without the dentate structure found in that species.

H. femoralis Eaton.

In this species the lobes, while distinctive in shape, resemble somewhat those of *H. simulans*, their perforate portion thickly clothed with cuticle hairs and containing a layer of epithelial cells into which the stalks of these cuticle hairs project. Attached to the inner face of the lobe there are numerous heavily ribbed androconia, the stalks of which pass through the chitin and communicate with an epithelial layer beneath. These androconia stain very deeply, have an oval section, and a small central lumen. The lobes cover two large eversible brushes provided with black hairs, the latter being considerably expanded at their distal extremities.

The brush bag appears to have much less glandular development than in *H. simulans*. The hairs are quite characteristic in structure, being very thick walled and covered on the outer surface with whorls of regularly arranged projections. Figs. 22 and 24. In many of the transverse sections of these hairs there is a slight staining of the central lumen indicating the presence of some structureless material in that position, probably a coagulated secretion.

Fig. 25 shows a section through the entire head of this species. At the lower side of the figure may be seen the lobes with part of the cellular material they contain, and their perforate external surface. Within the inner boundary are a few of the androconia cut across and portions of the brushes cut obliquely. Fig. 21 is a view of the entire head with brushes partly everted.

H. occulta Eaton.

The organs in this species are more remarkable than in any of the others examined. The lobes are narrow and somewhat conical. They bear on the inner surface a membrane, which towards the upper extremity contains a deep tubular pocket lined with long androconia. This pocket forms in fact a miniature eversible brush bag and can be extended so as to form a small secondary brush, the androconia then radiating from its surface. Besides this structure there are a few small androconia near the apex of the inner surface of the lobe, and arising from a point near the base is a third mass of androconia still more elongated than those already referred to. Sections of the lobe show that this second mass of androconia also lies in a small pocket and can presumably be everted. Both androconia pencils are surrounded by glandular tissue. Text fig. 2 shows a section through part of a lobe. At this plane the section shows chitin on the inner surface of the lobe. Apparently the eversible membrane as a whole only covers a part of the surface.

Lying beneath the lobes and arising from a membrane on the back of the head are two small eversible brushes with yellow hairs resembling those in *H. simulans*, but their sockets are more concentrated towards the bottom of the bag. The hairs themselves appear to have a structure somewhat similar to that in *H. forcipata*. There are also two small tufts of androconia arising from the membrane between the main brushes and on either side of the centre line. The general arrangement of the head with expanded organs is shown in text fig. 1, herewith. Fig. 11 shows one of the brushes dissected out. Fig. 13 a view of the lobe, the secondary brush being in a retracted condition. Fig. 14 represents one of the androconia from the secondary brush.

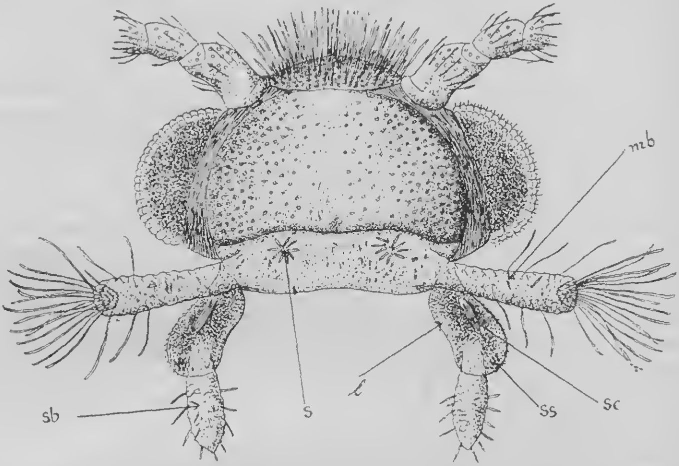


Fig. 1.—*Hydroptila occulta.* Head with scent-organs everted. *sb*. Secondary brush. *s*. Androconia. *l*. Lobe. *sc*. Patch of elongated androconia. *mb*. Main brush. *ss*. Small androconia. (Width across eyes ·64 mm.)

It is hoped that in the course of time other species than those so far examined will be available. Mr. Mosely has in his collection two examples of *H. pulchricornis* Pict., but beyond the fact that this species has black brushes resembling those in *H. femoralis* he has not been able to examine them more critically. There are other British species and several not so far found in Britain, and doubtless many new forms still undiscovered. But few collectors are interested in these small and inconspicuous insects. Now that Mr. Mosely's discovery has revealed their curious and interesting features collectors will have a new incentive to secure examples.

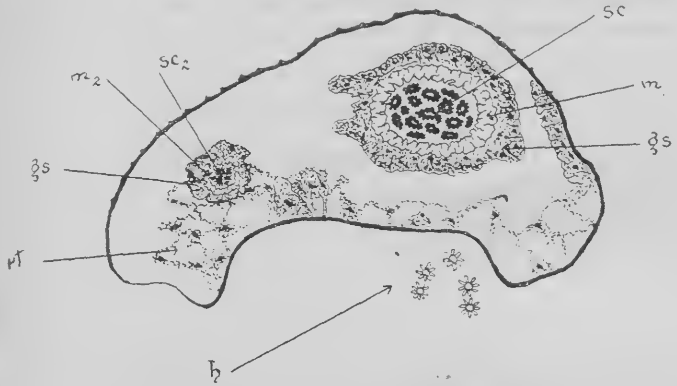


FIG. 2.—*Hydroptila occulta*. Section of lobe.

sc_2. Androconia of second tuft. m_2. Membrane of ditto. *rt*. Reticulated tissue. *sc*. Androconia of secondary brush. *m*. Membrane of ditto brush bag. *gs*. Glandular substance. *h*. Hairs of primary brush. (Length of section ·072 mm.)

In case this paper should be read by any one having facilities for securing further material, it should be noted that dry specimens are useless for observation. They should be dropped alive into a strong solution of bichloride of mercury in distilled water, to which has been added about half its bulk of 96 per cent. alcohol, and about 1 per cent. of acetic acid. After a few hours in this they should be transferred to clean 96 per cent. alcohol.

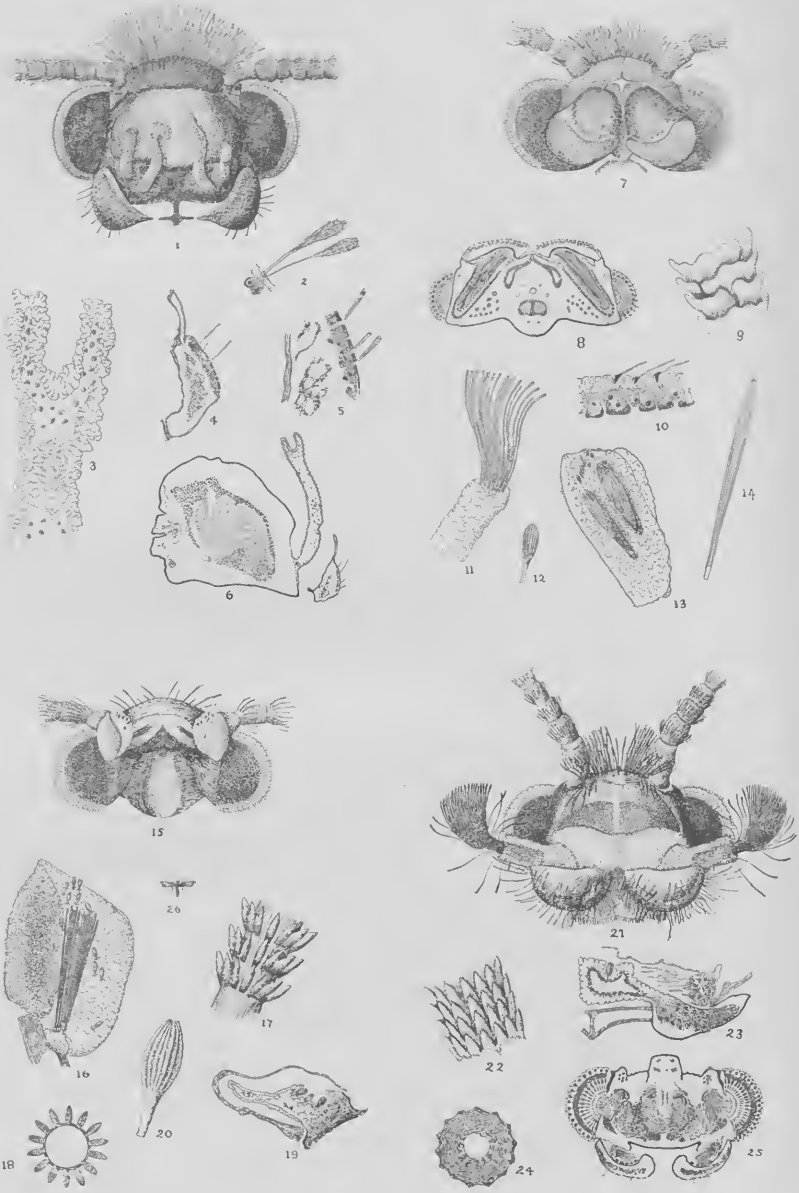
On the page facing the plate I have given the actual sizes of the various parts figured. A certain combination of objective and eyepiece may give a definite magnification, but when a figure has been drawn therefrom the size of the figure may not really represent the true magnification, but a mere expansion of the view obtained with the objective used. A photograph of a section measuring two inches across may represent a magnification of a hundred diameters, but the same photograph projected on a six-foot screen is not a magnification of three thousand six hundred diameters, but merely an enlarged view of what can be seen in the original photograph.

I have already expressed my thanks to Mr. Mosely for having supplied the material for this investigation, and I would add that he has further assisted by visiting Oxford on several occasions to compare the results with his previous knowledge of the species.

EXPLANATION OF PLATE XXII.

[*See Explanation facing the* PLATE.]

Westwood Bequest. *Trans. Ent. Soc. Lond., 1919.* Plate XXII.



H. Eltringham del.

SCENT ORGANS IN *HYDROPTILA*.

EXPLANATION OF PLATE XXII.

FIG. 1. *Hydroptila sparsa.* Head viewed from above showing four eversible tubercles partly expanded. Width across eyes ·6 mm.

2. Two of the androconia with their sockets and glands. Length from bottom of socket to apex of scale ·03 mm.

3. Enlarged view of one of the tubercles partly expanded. Width in narrowest part ·015 mm.

4. Section through one of the lobes. Length ·15 mm.

5. Part of ditto (not necessarily the same section) showing epithelium and parts of cuticle hairs. Greatest width ·03 mm.

6. Section through head showing one of the tubercles partly everted. Length of tubercle ·18 mm.

7. *Hydroptila simulans.* Head with lobes closed. Width across eyes ·77 mm.

8. Section through same in plane of brushes. Width across eyes ·6 mm.

9. Part of one of the brush hairs showing structure. Greatest width ·003 mm.

10. Enlarged view of brush bag showing hair sockets and epithelium. Greatest thickness ·015 mm.

11. *Hydroptila occulta.* Part of a brush. Length of hairs ·22 mm.

12. A small androconium from lobe of same. Length ·015 mm.

13. View of inner surface of lobe of same with secondary brush retracted, scent-scales, etc. Greatest length ·15 mm.

14. One of the scales of the secondary brush. Length ·06 mm.

15. *Hydroptila forcipata.* Back view of head with expanded lobe membranes and hair tufts. Width across eyes ·58 mm.

16. One of the lobes viewed from inner side. Length ·176 mm.

17. Part of one of the hairs. Diameter of main stalk ·003 mm.

18. Transverse section of same. Diameter over projections ·005 mm.

19. Section through one of the lobes showing gland cells at base. Length from end of membrane to upper corner of lobe ·09 mm.

Explanation of Plate.

FIG. 20. *Hydroptila maclachlani.* A scent-scale from lobe. Length ·015 mm.

21. *Hydroptila femoralis.* Head with brushes partly expanded. Width across eyes ·473 mm.
22. Part of a brush hair. Width across points ·003 mm.
23. *Hydroptila maclachlani.* Section through lobe, etc., showing glandular base. Length from point of membrane to point of lobe ·105 mm.
24. *Hydroptila femoralis.* Transverse section of hair. Diameter ·0015 mm. to ·0037 mm.
25. Section through head. Width across eyes ·55 mm.
26. Diagrammatic figure representing about the natural size of *H. femoralis.*

Reprinted from "The Entomologist's Monthly Magazine," 2nd Series, Vol. xxiv.

EMPIDÆ
AND THEIR PREY IN RELATION TO COURTSHIP.

Communicated by Professor E. B. Poulton, D.Sc., M.A., F.R.S.

The following observations by Mr. A. H. Hamm, of the Hope Department, Oxford University Museum, will, we feel sure, be of special interest to our readers. The account is reprinted from Professor E. B. Poulton's Report on the Hope Department for the year 1912 in *The Oxford University Gazette* for June 4th, 1913, pp. 952–953 :—

"No more interesting and valuable addition to the bionomic series has ever been made than the large collection by which Mr. A. H. Hamm, of the Hope Department, has thrown so much light upon the courtship of the Empid flies.

Results so surprising require abundant proof, and it will be admitted by any one who studies the series that the material both of *Empidæ* themselves and the insects captured or objects seized by them, is of immense extent and most carefully collected, embodying the results of a large number of original observations and most ingenious experiments. The whole of Mr. Hamm's researches were carried out in the neighbourhood of Oxford. The great labour of labelling and cataloguing was finished by Mr. Collins in time for exhibition at the Entomological Congress in August, 1912, where the collection was studied with keen attention and interest. The catalogue numbers—591 in 1908, 771 in 1909, 718 in 1910, and 969 in 1911, large as they are, give a very inadequate idea of the material; for the catalogue is of mounts rather than specimens, of which many are constantly carried on a single card. The collection includes many specimens captured and presented by Mr. Hamm's son, Mr. C. H. Hamm.

A part of the results has been already published in the 'Entomologist's Monthly Magazine' for 1908, p. 181, and 1909, pp. 132 and 157; but the most novel and interesting observations and conclusions —those obtained with the genus *Hilara*—are made known for the first time in the following brief account of Mr. Hamm's gift. The full and detailed account awaits publication until numbers of obscure and minute insects—Dipterous captors and prey chiefly Dipterous—have been satisfactorily worked out.

The collection has been classified by Mr. Hamm so as to illustrate his conclusions, the species being arranged in groups, each representing a definite evolutionary stage in the use of prey—first and lowest as food devoured by both sexes without relation to pairing, then as a gift provided by the male and devoured by the female during pairing, finally—as it were an ornament or plaything—no longer eaten by the female, but acting as a lure and a stimulus. In this last stage the prey is often replaced by some vegetable fragment which is quite unsuitable as food. The climax of this line of evolution is reached in an elaborate cocoon spun by the male around the prey and replacing the latter as an object of attraction. This replacement is self-evident in many examples studied by Mr. Hamm; for in these there was nothing but an empty cocoon, the prey having probably been lost during the process of construction.

There are strong reasons for the belief that the last stage has been reached through the second, and the second through the first, but this inference must not be extended further and made to apply to the species themselves.

I.—Prey devoured by both sexes independently of pairing.

A. *Tachydromia* (*Tachydrominæ*). Prey very nearly always Dipterous and often belonging to the genus *Tachydromia*, perhaps sometimes to the same species as the captor. The female *in copula* has very rarely been found with prey. 1908—ninety catalogued specimens (or mounts) of which 17 were captured by Mr. C. H. Hamm; 1909—eighty-six of which 2 were captured by Mr. C. H. Hamm; 1911—thirty.

B. *Hybos* (*Hybotinæ*). Prey generally Hymenopterous. 1908—eighty-four of which 26 were captured by Mr. C. H. Hamm; 1909—two; 1911—six.

C. *Empis trigramma*, *punctata* and *scutellata* (*Empinæ*). A little group of related species with habits very different from those of the rest of the genus so far as it has been studied. 1909—sixty-three.

II.—THE PREY PROVIDED BY THE MALE IS DEVOURED OR SUCKED BY THE FEMALE DURING COPULATION.

A. *Pachymeria* (*Empinæ*). The prey always Dipterous. 1908—one hundred and ten; 1909—one hundred and seventy-eight.

B. *Rhamphomyia* (*Empinæ*). The prey nearly always Dipterous. 1909—three; 1910—two hundred and fifty; 1911—sixty-five.

C. *Empis* (*Empinæ*). Small species as yet undetermined. Prey nearly always minute *Diptera*, chiefly *Cecidomyia* and *Psychodes*. 1909—two; 1910—fifty-five; 1911—one hundred and three.

D. *Empis tessellata*. Prey very varied, but always Dipterous. 1908—two; 1909—two hundred and twenty-four; 1910—twelve; 1911—thirty-three.

E. *Empis opaca*. Prey like that of *tessellata*, but mainly of the genus *Bibio*. 1909—one hundred and sixty-eight; 1910—forty-six; 1911—forty.

F. *Empis livida*. Prey more varied than that of any other species of the genus, but still chiefly Dipterous. 1908—three hundred and five, of which 4 were collected by Mr. C. H. Hamm; 1909—forty-five; 1911—thirty-two.

III.—THE PREY OR OBJECT PROVIDED BY THE MALE IS NOT DEVOURED BY THE FEMALE, BUT BECOMES, AS IT WERE, AN ORNAMENT OR PLAYTHING PROVIDING SOME INDISPENSABLE STIMULUS.

A. *Hilara* (*Empinæ*). Many species as yet undetermined. All the species fly over water, and the prey or other object is always picked up from its surface by the male *Hilara*. The males take floating insects of all kinds - sometimes specially *Diptera*, sometimes Aphids—scales off overhanging trees or other fragments of plants. Some of the species will accept almost any floating object, while others seem to restrict themselves to particular insects, such as *Aphidæ*. When the object is very heavy, the male, after seizing it, spins round with great velocity till the load rises on a cone of water, and is finally lifted from the apex. In Mr. Hamm's experiments, disabled *Diptera* of the genus *Chironomus*, &c., stamens of buttercups, and ray florets of daisies strewn on the water were soon taken by the males, and afterwards found in the possession of the females. Pairing invariably occurs upon the wing, but numbers of specimens show that a sweep of the net through the swarm at first catches nothing but males carrying the objects that had been strewn on the water, while a later sweep catches pairs still carrying the same objects. The specimens illustrating this investigation are all carefully labelled with the hour and minute at which the different samples were secured.

Mr. Hamm's admirable experiments also enabled him to determine that the females carry the objects provided by the males; for although they are never retained when the pairs are captured, the white florets or the yellow stamens can be seen hanging from the lower *Hilara* of each flying pair, and the lower is invariably the female.

The climax is reached in the males of certain species of *Hilara* which envelope the prey or other minute object in a cocoon, varying greatly in complexity, but in the most extreme cases of striking beauty and regularity. The cocoon is spun upon the wing, so that the method of its construction cannot be followed. Captured individuals are often found to have extruded a viscid globule—probably the material out of which the cocoon is spun. There can be little doubt that in these extreme cases it is the cocoon itself which acts as a stimulus to the female, although the minute and almost invisible object usually enclosed in it, but sometimes dropped, is the stimulus which incites the male to spin. Cocoons that have been dropped, probably after pairing, are constantly picked up and used over again by other males.

These novel and surprising conclusions, obtained as the outcome of Mr. Hamm's energy, resource, and power of accurate observation, are illustrated and confirmed by an immense mass of mounted material, catalogued under 355 numbers in 1910, and no less than 660 in 1911."

[*Reprinted from the 'Entomologist's Monthly Magazine,'* 3rd ser., vol. v.]

A RIBBON-MAKING FLY:
THE OVIPOSITION OF *CERATOPOGON NITIDUS* MACQ.

BY A. H. HAMM, F.E.S.

For a few days last August I was spending part of my holiday at the picturesque little village of Woolhampton, near Newbury, Berks. The evening of the 13th was very warm and sultry, and the various "biting" flies, such as *Anopheles*, *Culex*, *Ceratopogon*, and *Simulium*, were feasting upon all and sundry. I often had three or four *Culex pipiens* on my hand at one time, but, fortunately for me, their "bite" leaves no after-effect.

I was patiently watching, on the bank of a stream running through one of the numerous osier-beds that are such a feature of this part of the Kennet Valley, several species of *Hilara*, especially *H. lurida* and *H. nigrina*, the males of which were very busy catching their "prey" and afterwards going through their usual courtship tactics. It was while thus occupied that I noticed, hovering above the surface of the stream, a fly that had something white hanging beneath it. Thinking it was another species of Empid with "prey," I netted and boxed the fly, and then recognised it as a *Ceratopogon*. I then made a hasty examination with a lens of the object which the fly had dropped in the net, and was surprised to find it was a gelatinous ribbon of ova. I then saw and netted several other flies hovering over the stream, with similar ribbons. They hovered (with little or no perceptible movement) about two feet above the stream and then immediately began the work of ribbon-making. By patiently watching one could observe the operation, occupying about three minutes, from start to finish. Gradually the ribbon, hanging vertically from the very start, would lengthen, until the full number of ova had been extruded. I could not determine whether the legs contributed in any way by holding and paying out the ribbon during its extrusion; for nearly all the flies kept in mid-stream, and the light, just before sunset, was none too good. When its full length was attained the fly, still poised motionless in the air, dropped the ribbon into the stream beneath, where it gradually sank as it was borne along by the fairly rapid current.

The following measurements, for which I am indebted to my friend Dr. Eltringham, were made from a dry and probably shrunken ribbon, which, moreover, was not of maximum length, as the fly was netted before its completion:—

Length of ribbon, 19 mm. Width of ribbon, ·22 mm.

There are 30 ova per mm., making 570 ova in all.

The eggs, which lie obliquely across the long axis of the ribbon, are, when fresh, white with a faint yellow tinge.

Mr. F. W. Edwards, to whom the mode of oviposition was unknown, has kindly identified the species as *Ceratopogon nitidus* Macq., and has drawn my attention to an interesting and somewhat analogous procedure on the part of an American species, as described by O. A. Johannsen in the 58th Annual Report of the New York State Museum, 1904, vol. v, p. 107:—

"AQUATIC NEMATOCEROUS DIPTERA.—II.

"*Sphaeromyas argentatus* Loew.

"The egg-laying of this species was first observed by Professor Needham, by whom my attention was called to it. During the latter days of June and the first of July about sundown, the female fly hovers about three or four inches above the water's surface close to the shore in a place sheltered by the shrubs and weeds. With the head pointing towards the shore and the body swaying rhythmically laterally to and fro, the egg-laying begins. The eggs are enclosed in a gelatinous ribbon, placed at right angles to the long axis. . . . The ribbon when deposited is about 1·5 inches in length, flat, and appears wrinkled like a paraffin ribbon. The lateral swaying of the body at the beginning of the egg-laying is of about one inch amplitude, but as the ribbon of eggs increases the amplitude decreases, until just before deposition it is less than ½ inch. When the egg-string is about ¼ inch long the fly seizes it with her hind and middle legs, the hind legs guiding, the middle legs paying out the string as its length increases. The fore legs are folded up under the body. This egg-laying process occupies from three to five minutes; when completed the fly suddenly darts down to the water's surface, deposits her eggs and flies away.

"The eggs when first laid are whitish, but later, as development progresses, they become brown. Each egg is about 0·4 mm. in length by ·07 in width; somewhat pointed at one end and flattened at the other, the latter with a minute rectangular bolster with knobbed corners."

22 Southfield Road, Oxford.
February 13*th*, 1919.

[*Reprinted from the* '*Entomologist's Monthly Magazine,*' 3rd ser., vol. v.]

OBSERVATIONS ON THE HORSE BOT-FLY, *GASTROPHILUS EQUI* F.

BY A. H. HAMM, F.E.S.

The phenomenally fine and hot weather during the first half of August last was evidently highly favourable to that well-known pest, the Bot-fly (*Gastrophilus equi* F.). My holiday falling within the same period enabled me to give some attention to and make a few observations on this species.

On August 7th, in Hogley Bog, near Oxford, I netted one male and two females from round the legs of a mare turned out to grass. The flies are very easy to catch if only the horses will stand still for a moment and allow one to approach; but this was by no means easy, for at the least movement of the net the horse invariably galloped away, so that the stalking had to be begun over again. However, with persistence and patience the three specimens were at length secured. The number of eggs laid on this particular horse was truly astonishing. From below the knee to just above the hoof they were so close together that they entirely covered the hair on the anterior surface of the fore legs. Many were also laid on the hind legs, shoulders, hind-quarters, and a few even on the mane. I drew the owner's attention to her condition and he promised to do what he could to remove them. I had another look at her on the 10th when she was fairly free from eggs, and no bot-flies were in attendance. I did not see her again until the 23rd, which was a very dull and not over warm day, but the eggs that had again been deposited were equally or even more numerous than those observed on the 7th.

On August 10th on Lye Hill, adjoining Hogley Bog, a number of farm horses, turned out to grass, were all huddled together under the shade of some large elm trees, and owing to the presence of *Haematopota* and various other flies they were extremely restive. They allowed me, however, to approach near enough to see that several female bot-flies were busy ovipositing. Every horse had a large number of eggs attached to various parts, mostly the fore legs below the knees.

On August 11th I went to Newbury for a few days. Crossing Victoria Park, close to the town, on the 16th, I saw a group of four or five horses close together in the shade of an avenue of lime trees. The shrill bee-like hum of the bot-flies in attendance about the horses' legs was perfectly audible at several yards distance. By dint of patience and caution I secured five specimens, all females. All the horses were much infested with their eggs, as before mainly on the fore legs, below the knees. At various places in the neighbourhood I examined many horses employed in harvest operations, and found most of them badly infested.

I went over to Woolhampton, 6 miles from Newbury, on August 14th, and on the following day saw several horses under elm trees in a field. A few bot-flies flying round their legs rendered them extremely restive, so much so indeed that at the least flick of the net they would scatter at full gallop round the field, returning again later to the same spot for the shade. The bot-flies apparently accompanied them on their gallop, for no sooner did they stand still than they were subject to the same attentions as before. At Woolhampton I examined many horses at work, or turned out to feed, and found, as at Newbury, most of them badly infested with eggs.

Though I closely watched the flies many times and for considerable periods, I never saw one settle on a horse. Their mode of ovipositing is to hover close to the animal, the body approaching the vertical; then, still hovering, the long ovipositor-like abdomen is turned upwards to attach the egg to the hair. The horse seems fully conscious of the fly's intention, for no sooner does the tip of the abdomen touch the animal than it gives a twitch or brings its head to the threatened spot, or a flick of the tail if on the hind-quarters or hind legs. Though driven off for the moment, the fly returns and succeeds by her persistence, and so absorbed is she that capture would be extremely easy if only the horse would stand still.

I have heard it stated that shade gives the horse some relief from these attacks, but so far as I observed little or no protection is afforded by it.

22 Southfield Road, Oxford.
September 11*th*, 1919.

AN ADDRESS

READ BEFORE THE

ENTOMOLOGICAL SOCIETY OF LONDON

AT THE

ANNUAL MEETING

ON THE

21 ST JANUARY, 1920.

BY
COMMANDER JAMES J. WALKER, M.A., R.N., F.L.S.
President of the Society.

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1920.

THE PRESIDENT'S ADDRESS

LADIES AND GENTLEMEN,

FROM the Report of the Council which has just been read, it is I think fairly evident that the past year has been one of more than usual prosperity for our Society. Not only do our finances—thanks in large measure to our energetic Treasurer—show a balance in our favour that may be regarded as highly satisfactory, but the steady increase in the numerical strength of the Society during the past session is most encouraging, and the number of new Fellows elected on December 3rd has only once been exceeded, I believe, at any previous meeting.

With one exception of recent date, due to causes entirely beyond our control, in which the number of Fellows present reached probably the lowest point in our entire history, our meetings have been very fully attended, and the exhibits and discussions have been quite up to their usual high standard. Notwithstanding the fact that the cost of printing, and even more that of illustration, continues to grow by leaps and bounds, the Transactions and Proceedings of the Society for the past year, though they may not attain the bulk of some of our former annual volumes, are not a whit behind any of their predecessors in scientific value and interest. Among so many meritorious papers it is perhaps invidious to draw special attention to any one of them; but we may congratulate ourselves on being enabled to publish in our Transactions a memoir on so suggestive and interesting a subject as the paper by Dr. Eltringham on "Butterfly Vision."

Our Library continues to increase steadily, and the difficulties arising from the inadequate space in which we are compelled to house it become more painfully evident year by year. The necessity of seeking more ample accommodation is thus in a measure forced upon us; and although some, including myself, may regret having sooner or later to leave our present quarters, with their advantages of central situation and ready accessibility, and their associations with the memories of forty-five years of the Society's history, we can only trust that our efforts in that direction may be crowned with success in the near future.

The honour you have conferred upon me by my election to the office of President has involved the choice of a new Secretary in my place, and the Society may be congratulated in having found in Dr. S. A. Neave a Fellow who has proved himself so highly qualified in all respects for this somewhat onerous but highly interesting and enjoyable office – I speak from experience. To Dr. Neave and his colleague the Rev. G. Wheeler, as well as to the other Officers and Members of Council, my best thanks are due for their steady and unfailing support and assistance during the past session.

I regret to say that our losses by death have been more numerous than usual, and two of our Fellows who have gone from us were in the very front rank of Entomological Science, and in former years were among the most distinguished occupants of the Presidential Chair. On February 19th Dr. F. Du Cane Godman passed away, full of years and honours, and the generous appreciation by Lord Walsingham of his life-work and personality, read by me from the Chair at the meeting immediately after his death, is still fresh in the recollection of all of us. We may, I think, agree that this noble tribute to the memory of our late valued colleague applies in very large measure to its own writer, whose unexpected decease on December 3rd it was my painful duty to announce to the Society at our meeting on the same evening. I fear it will be long indeed before the places of these two great masters of our Science can be adequately filled.

We have also to regret the loss of the veteran Major Thomas Broun, whose great work on the beetles of New Zealand, continued through many years, has revealed to us the marvellous Coleopterous fauna of those most interesting islands in the far South; of Hereward Dollman, a young and highly promising Entomologist and an accomplished artist, whose premature death was the result of a fell disease contracted in the course of duty in Tropical Africa, and of W. E. Sharp, one of the most able and energetic students of British *Coleoptera*, until quite lately a familiar figure at our meetings, and whose genial and sympathetic nature endeared him to all of us. We rarely saw Sir Frank Crisp, who joined the Society as long ago as 1880, and who was perhaps best known as an eminent microscopist and botanist, as well as a tower of strength to the Linnean Society. Other Fellows who have passed from among us are Lt.-Col. L. Blaythwayt, G. M. Carson, H. A. Fry, F. Hannyngton, T. Nottidge, E. J. Patterson, S. Wacher, and F. H. Wolley-Dod, the last-named being distinguished for his researches and observations on the Lepidoptera of the western regions of British North America.

It is perhaps a natural result of my career in the Royal Navy, in which I had the good fortune to observe and to study insect life, however superficially at times, in many remote and rarely visited parts of the world, that the subject of Geographical Distribution has always appealed to me more strongly than has any other aspect of our Science. On the present occasion it has occurred to me that a useful purpose may be served, by bringing together as many as possible of the available records of those hardy and adventurous butterflies which have penetrated northward and southward to the extreme limits of terrestrial life, and to the most remote islands in mid-ocean. I therefore venture to suggest, as the title of my Address—

"The Fringes of Butterfly Life."

Commencing our circuit of the shores of the North Polar Ocean with Norwegian Lapland, we find here a butterfly fauna of unexpected richness and variety for so high a latitude. Our enterprising Fellows, Messrs. Rowland-Brown and Sheldon, have in recent years visited this very interesting region, and we are greatly indebted to them for their delightful and valuable papers on Lapland butterflies in the volumes of the "Entomologist" for 1906 and 1912. Herr J. Sparre-Schneider enumerates no fewer than forty-six species which extend their range beyond the Arctic Circle, and of these such familiar forms as *Papilio machaon*, *Pieris brassicae* and *napi*, *Callophrys rubi*, *Vanessa antiopa* and *urticae*, the almost world-wide *Pyrameis* *cardui*, *Argynnis aglaia*, *Brenthis euphrosyne* and *B. selene*, are found as far north as the 70th parallel of latitude. Still more characteristic of the Arctic fauna are *Colias hecla*, Lef., *Erebia disa*, Thunb., *Oeneis norna*, Thunb., *Melitaea iduna*, Dalm., *Brenthis chariclea*, Schneid.—perhaps the rarest of European butterflies—*B. frigga*, Thunb., and *B. polaris*, Boisd., most of which we shall frequently encounter again as we proceed eastward round the Polar basin. Another of our Fellows, Dr. Cockayne, has by the fortune of war been enabled to gather some experience of the butterflies of the Murman coast, and we may, I hope, look forward to an account of his observations in that practically unknown region. Dr. B. Poppius records six species, all well-known Lapland forms, from the Kanin Peninsula east of the White Sea; and on August 4th, 1879, on the east coast of Novaya Zemlya, facing the inhospitable Kara Sea, the late Admiral Sir A. H. Markham met with *Colias nastes* var. *werdandi*, Zett., *Brenthis chariclea*, and the remarkable *B. improba*, Butl., which is probably a melanic form of *B. frigga* and was previously known only from Arctic America. Concerning these butterflies he writes—" The land at the head of Schubert Bay was the only place where I saw butterflies; and here I was fortunately able to secure several different specimens. They are, I believe, the first captured and brought home from Novaya Zemlya. They were excessively wild, flew very fast, and rarely alighted, so that they were exceedingly difficult to catch. . . . It is a curious fact that, although I landed several times during the month of August with the express purpose of obtaining specimens, it was only on the day above referred to that I saw any."

Records from the northern shores of Siberia are nearly or quite wanting, but the adventurous German explorer Middendorff gives a vivid and graphic description of the summer aspect of the tundra in the Taimur peninsula, gay with innumerable flowers and alive with insects, of which unfortunately the vast majority are the notorious Siberian mosquito. Middendorff tells us that on August 3rd, 1845, in the very middle of the short Taimurian summer, in 74° 15′ north latitude, he hunted butterflies under the shelter of a hill, barefooted and in light underclothes. The thermometer rose in the sun to + 68° F., and close to the ground to + 84°, while at a short distance on a spot exposed to the north-eastern air-current, it fell at once to + 27°. Further he states that "the more vigorous vegetation on the sheltered declivities of the Taimur provides food for a greater number of insects than is found on the coasts of Novaya Zemlya. Bees, hornets, and three species of butterflies, buzzed or hovered round the flowers, and caterpillars could be gathered by dozens on the tundra; but their mortal enemies had pursued them even here, and ichneumon flies crept out of most of them."

Many degrees of longitude to the eastward, the naturalists of the "Vega" expedition, during their memorable "Northeast Passage" in 1878–9, found at their winter quarters, about 100 miles west of Behring's Strait, "larvae of an *Argynnis*" at the end of June; and they met with *Oeneis crambis*, Freyer, and *Erebia rossii*, Curtis, at St. Lawrence Bay in Chukchi Land, a little to the southward of these Straits. The swampy meadows of the desolate Pribyloff Islands, in the middle of Behring's Sea, are, according to H. W. Elliott, enlivened in summer by myriads of yellow butterflies, in all probability one of the North American species of *Colias*. Alaska appears to possess a fairly rich butterfly fauna, two Papilios, *aliaska*, Scudd., and *turnus*, L., even extending to the valley of the Yukon, from whence thirteen species of butterflies are recorded by Dr. S. H. Scudder. I can find no records, however, from beyond the Arctic Circle in this region, except that of *Erebia fasciata*, Butl., which appears to be not rare at Kotzebue Sound. This remarkable species was first obtained at Cambridge Bay (lat. 69° N., long. 107° W.) by Capt. Collinson in H.M.S. "Enterprise," during the prolonged search for Sir John Franklin's lost expedition. Mr. D. Hanbury, in the summer of 1902, made a large collection of butterflies on the Arctic coast near Cape Barrow (lat. 68° 30′ N., long. 111° W.), which is described by our former President Mr. H. J. Elwes in our Transactions for 1903, and illustrated by a very fine coloured plate. This collection, probably the most interesting and representative series of Arctic butterflies ever obtained from any one locality, consists of no fewer than fifteen species, including three *Erebias* (*fasciata*, Butl., *disa*, Thunb., and *rossii*, Curt.); two *Oeneis* (*bore* var. *taygete*, Hübn., and *semidea*, Say, var.); a variety (*mixturata*, Alph.) of our *Coenonympha typhon*; four species of *Brenthis* (*pales*, W. V., *polaris*, Boisd., *chariclea*, Schn., and *frigga* var. *improba*, Butl.); *Lycaena orbitulus* var. *franklinii*, Curt.; and four species of *Colias* (*hecla*, Lef., *boothii*, Curt., *pelidne*, Boisd., and *nastes*, Boisd.). From a little farther to the north-east, on the shores of Prince Regent's Inlet, we have the insects collected and preserved under the most trying conditions by the expedition under Capt. Sir John Ross, in the "Victory" during its sojourn of four years (1829–1833), in this desolate region; the second officer in command, afterwards Sir James Clark Ross of Antarctic renown, being in most cases the actual collector. Five species of butterflies are described and figured by John Curtis in his inimitable style, in the Appendix to Sir John Ross's Narrative of this voyage. These are *Colias boothii*, which "appears in mid-July on *Oxytropis*;" *C. chione*, probably a variety of the preceding; *Hipparchia* (*Erebia*) *rossii*, "five only, they were scarce and frequented the precipitous faces of dark-coloured rocks and loose stones; I never found any of them on flowers of any kind" (J. C. Ross, 1830); *H.* (*Oeneis*) *subhyalina*, one only, probably with the preceding; *Melitaea tarquinius*, in all probability the widely ranging *Brenthis chariclea*, "an abundant species, like the *Coliades* found feeding on the flowers of *Oxytropis*, June and July 1830"; and *Polyommatus franklinii* (= *orbitulus*, Esp. var.), "only two taken, feeding on *Astragalus alpinus*, end of July."

Another British Arctic expedition of more than forty years later date, that under Sir George Nares in the "Alert" and "Discovery" in 1875–6, brought back an important little collection of insects from nearly the highest latitude attained on that occasion, and the butterflies included in it may be regarded as probably the most northern representatives of their race in the world. Our former President, Mr. R. McLachlan, writes of these insects as follows—"Thirty-five specimens of gaily-coloured butterflies were procured, belonging to certainly five distinct species. It may safely be asserted that there are desert regions in the tropics that would not furnish an equal number. I have used the term 'desolate';

but the desolation is not of that extreme nature one would expect. I am informed by Prof. Oliver that over sixty species of flowering plants have been determined in the collections formed by the naturalists of the expedition between the already given parallels of latitude (78° — 83° N.). This fact, at first sight, reads like romance . . . Captain Feilden informed me that during the short period when there is practically no night, butterflies are continuously on the wing, supposing the sun's face not to be obscured by clouds or passing snow-showers." The species found in the vicinity of the "Discovery's" winter quarters, between 81° 42′ and 81° 52′ N. latitude, were *Colias hecla* (var. *glacialis*, McL.), *Brenthis polaris* (also from Disko Island in lat. 70° N.), *B. chariclea*, *Lycaena orbitulus* var. *aquilo*, Boisd., and, strange to say, a slight aberration (*feildeni*, McL.) of our familiar "Small Copper," *Chrysophanus phlaeas*, L.

Some very interesting observations on the butterflies of this remote region were also made by Lieut. A. W. Greeley, the leader of the ill-fated American Polar expedition of 1881–4. At Lake Hazen, in the interior of Grant Land, on June 28th 1882, "a large number of butterflies were seen, of which there were apparently three different species. They were so active and distrustful, however, that I succeeded in capturing but one during the day." On the 29th, one of the party saw "a bumble-bee and a devil's darning needle"—a highly interesting record, showing that the range of the *Hymenoptera* and the *Odonata* extends as far to the northward as that of the *Lepidoptera*—and "butterflies were very numerous, as many as fifty being seen during the day," which was one of unprecedented high temperature in the Far North.

The intrepid American explorer R. E. Peary also contributes his quota to the records of these Hyperborean butterflies. In June 1892, after he had crossed the appalling ice desert of North Greenland to bare land on the north-east coast, elevated 3800 feet above the sea, in lat. 81° 37′ N., long. 34° 5′ W., a fair amount of vegetation and "two bumble-bees, several butterflies, and innumerable flies" were noted by him. Another American Arctic voyager, Dr. I. I. Hayes, records the capture of a "yellow-winged butterfly" on July 9th, 1861, at his winter quarters at Port Foulke (lat. 78° 17′ N., long.

73° W.); and a few days later, at Barden Bay in Whale Sound (lat. 77° N.) "myriads of butterflies fluttered among the flowers," the day being calm and sunny, with the high temperature for that latitude of 51° F.

The entomologists of the Danish expedition to North-east Greenland in 1910, at the winter quarters of their ship on the east coast in lat. 76° 46′ N., long. 18° 14′ W., met with *Colias hecla*, *Brenthis chariclea* var. *arctica*, Zett., and *B. polaris* in numbers, and *Lycaena orbitulus* var. *aquilo* less commonly. One of them, Fritz Johansen, gives such a graphic and pleasing account of these butterflies in their almost inaccessible home, that I cannot refrain from quoting it *in extenso*. "Most marked of all the insects, however, are the butterflies, as it is only in the height of summer that all are out and can be said to be common. It is remarkable that with but few exceptions the North-east Greenland butterflies are not found on the most fertile places. On mossy ground, for example, the only common butterfly is the yellow *Colias hecla*, but this is also so much bound to such localities, that if there is a fertile slope round a larger or smaller water-course, we may be almost sure of seeing a *Colias* flitting about, and be able to follow with the eye how it keeps to the windings of the slope. On large grassy plots (for example at the foot of the fells) we see several of these beautifully coloured insects flitting about; when two come nearer together, they playfully cross and recross in the air before separating; the one perhaps settles on a *Dryas* blossom, whilst the other seeks rest on a blade of grass, the colour of which it resembles so much. The commonest day butterflies are, however, the *Argynnis*, but like the following they are not met with on boggy ground (nor in fact on the bare clay or stone plains). Yet we may be surprised by these butterflies flying up from ground where the dry grass, *Cassiope*, and other plants are only growing in hollows here and there, until we observe that it is just these places which afford the butterfly the most shelter. When this settles, for example, on a stone or a *Cassiope* tuft, the reddish-brown lichen covering the former, like the purple-black leaf of the latter, blends so perfectly in colour with the butterfly that this cannot be seen before it starts up. It is very shy, flying often far before it again settles, and as it 'doubles' a great deal in its flight, it is more difficult to catch than *Colias*. These butterflies are sometimes seen together, however, in which case it is *Argynnis* that has come on to the grounds of *Colias*, and they playfully cross one another before proceeding on their way. More rarely and more singly we meet with the day-butterfly *Lycaena orbitulus* on localities similar to those of *Argynnis*. It is quite impossible to see this butterfly when sitting on the ground; the gray underside of the folded wings blends so perfectly with the surrounding small stones. It does not fly far each time, but irregularly and fairly quickly."

A much earlier record of butterflies from the same coast, but in a considerably lower latitude, is that of the veteran whaling captain William Scoresby, junior. At the end of July 1822, in the region now known as Scoresby Sound (lat. 70° 30′ N., long. 22° W.), he found on landing that "the insects were numerous, consisting of mosquitoes, and several species of butterflies." These latter are named in the appendix to Scoresby's narrative of his voyage, as "*Papilio palaeno*, L., and *P. dia*, L.," by Prof. Jameson of Edinburgh. Many years afterwards (1899–1900) this part of the Greenland coast was visited by Prof. A. G. Nathorst, who there collected specimens of the four butterflies so characteristic of these high latitudes, *Colias hecla*, *Brenthis chariclea*, *B. polaris*, and *Lycaena orbitulus* var. *aquilo*, to the first two of which Scoresby's insects must in all probability be referred. No butterfly has been as yet recorded from Spitsbergen, though several species of moths are known from this archipelago.

Before finally leaving the North Polar basin, the case of Iceland demands attention. As many as six species of butterflies, belonging to the characteristic Arctic genera *Colias*, *Erebia*, and *Brenthis*, have been stated by various writers to occur in this large island, which from its relatively mild climate and fairly luxuriant vegetation might reasonably be expected to produce some at least of them. But of late years, the visits of several able entomologists to Iceland, notably the long stay of Dr. Staudinger in 1857, have not revealed the presence of even a single resident species. The only authentic record that I can find of the occurrence of any butterfly in Iceland, is that of the late Rev. Francis Walker, who notes in Vol. XXII of the "Entomologist," the capture by Jon Thoroddson in 1888 of a specimen of *Pyrameis cardui* in one of the main streets of Reykjavik, the capital of the island.

When we proceed to the Southern Hemisphere, we find the terminations of the great land-masses lying many degrees farther from the Pole than is the case in the north; and with the exception of the extremity of South America, these southern lands enjoy far more genial conditions of climate. But the scanty butterfly fauna of these regions, as compared with that of corresponding or even far higher latitudes north of the equator, has not failed to impress strongly all Entomologists who have studied the distribution of these insects. The marked contraction southwards of the African continent would appear to have crowded, within narrow limits at its extremity, a Flora unparalleled anywhere in variety and number of species, with the possible exception of South-western Australia, where the geographical and physical conditions are somewhat similar. But when the comparatively low latitude of both these regions is considered, their poverty in butterflies is most remarkable. Lapland, more than thirty degrees nearer the Pole, produces at least as many kinds of butterflies as does Cape Colony, and during a residence of twenty-five years at Cape Town our former President Mr. Roland Trimen could find only forty-seven species in the immediate neighbourhood. A very large proportion of these are inconspicuous forms of *Satyridae*, *Lycaenidae*, and *Hesperidae*, only one *Papilio* (*leonidas*, Fab.) extending its range so far south, and the fine Nymphalid *Meneris tulbaghia*, L., being almost the only showy butterfly. The fauna of Western Australia is even more scanty, as only fifteen species are enumerated as occurring in the district round Perth; and when I was there in the summer of 1890, I was as much impressed by the very small number of butterflies to be seen on the wing, as by the endless variety and beauty of the flowers. Next to nothing is known of the insects of the long range of utterly desert coast facing the great Southern Ocean, and the more fertile regions of South Australia and Victoria are not much richer than Western Australia in species. The beautiful, varied, and luxuriant island of Tasmania, larger in area than Scotland, has fewer than thirty species of butterflies, including two or three remarkable endemic mountain forms of *Satyridae* formerly referred to the characteristic Australian genus *Xenica*, as well as one *Papilio* (*macleayanus*, Leach) which is common near Hobart, and is the most southern representative of its almost world-wide family.

In Patagonia we find, east of the mountain backbone of the country, a barren and treeless land with a limited Flora and a rigorous climate for its latitude, while the densely forested coast facing the Pacific Ocean is one of the wettest and most stormy regions in the whole world. Butterflies are therefore very poorly represented, C. Berg recording only fourteen species as occurring south of the Rio Negro in lat. 40°. In the vicinity of Magellan's Straits some half-dozen species have been found, and *Colias imperialis*, Butl., one of the finest and rarest representatives of its genus, is supposed, though with some doubt, to have been taken by Capt. P. P. King, R.N., at Port Famine about the year 1830. When I was at Punta Arenas on Christmas-day 1880, I found the grassy park-like country near the settlement enlivened by numbers of three pretty butterflies, *Colias vautieri*, Guér. (var. *cunninghami*, Butl.), *Pieris* (*Tatochila*) *argyrodice*, Staud., and *Brenthis cytheris*, Drury; but insect life of any kind was almost absent in the gloomy and saturated forests of the Western Patagonian channels. Mrs. Scoresby Routledge, however, in her adventurous voyage in the yacht "Mana" to Easter Island in 1913, occasionally saw butterflies on the shores of the Messier Channel in lat. 49° S. In Tierra del Fuego, Darwin says that he "saw very few flies, butterflies, or bees," but *Tatochila theodice*, Boisd., *T. xanthodice*, Luc., and *Brenthis cytheris* are recorded by Mabille from Orange Bay in Hoste Island, not far from Cape Horn in lat. 55° 30′ S., and these are almost certainly the most southern of all known butterflies.

Brenthis cytheris is also reported by Mr. R. Vallentin as occurring commonly in the bleak and treeless Falkland Islands, and another "larger and faster flying Fritillary with more pronounced markings," which he says has been seen in West Falkland, is almost certainly *Danaida plexippus* (race *erippus*, Cram.) which has wandered hither from South America, and has been captured in the islands on more than one occasion. The "blue butterfly," stated by Mr. Vallentin to have been frequently observed close to Stanley in the East Island, has not been identified, and thus remains a mystery.

The butterflies of oceanic islands, as defined by Wallace, form the subject of the second part of this Address, and I purposely omit any allusion to those of such island groups as lie near the great continents, and the insects of which are more or less well known. Reference may perhaps be permitted to the Faroe Islands, from which no butterfly is definitely recorded as yet, though there is a strong probability that *Coenonympha typhon* at least may be eventually found there; and to St. Kilda, where *C. pamphilus* is the only species that has been noticed. From the Azores, lying far out in mid-Atlantic, the late Dr. Godman has recorded nine butterflies, all familiar British forms except *Danaida plexippus*, which was first observed there in 1863, and has occurred subsequently on several occasions. To these may be added the little-known *Satyrus azorica*, Strecker, which is perhaps identical with a Satyrid butterfly seen in October 1880 by one of my messmates in H.M.S. "Kingfisher" in some numbers among the rocks on the summit of the Caldera of Fayal, 3300 feet above the sea. I ascended the mountain on the following day, which was unfortunately cloudy, so not a single example of the butterfly could be seen. The one specimen brought to me was in poor condition, but it appeared to be more nearly related to *Oeneis* than to any other genus, and it is well worth looking for by any entomologist who may visit these interesting islands.

Fourteen species of butterflies, according to Prof. A. E. Verrill, have been observed on the coralline group of Bermuda, which is fully 600 miles from the nearest point of the coast of North America. The record of three of these, *Vanessa io*, L., *V. polychloros*, L., and *Debis portlandia*, F., rests on the evidence of single specimens said to have been taken in the islands by Canon Tristram as long ago as 1848; but the first two species, to say the least, are most unlikely to have found their way from Europe to Bermuda. *Vanessa antiopa*, L., *Callidryas eubule*, L., *Colias philodice*, Hübn., *Pieris rapae*, and *Papilio cresphontes*, Cr., are more or less infrequent stragglers from the American mainland, and *Terias lisa*, Boisd., which has on more than one occasion visited Bermuda in great swarms, has perhaps succeeded in establishing itself as a resident species. *Danaida plexippus* has long been known from the islands, and *D. berenice*, F., *Pyrameis atalanta*, *P. cardui*, and *Junonia coenia*, Hübn., are also resident, a fine and strongly marked race of the latter being the commonest Bermudan butterfly.

Fernando Noronha, though barely 200 miles from the nearest point of Brazil, and covered with trees and luxuriant vegetation, has only one little Lycaenid, a form of *Tarucus hanno*, Stoll. From Ascension, 750 miles distant from the coast of Africa, *Pyrameis cardui*, *Hypolimnas misippus*, and *Lampides boeticus* have been recorded by Mr. P. de la Garde, R.N., although the vegetation of the island is of the scantiest, except on the highest summit, where there is a little cultivation and some trees and shrubs have been planted. The more inviting and fertile island of St. Helena has but one species, *Limnas chrysippus*, in addition to those of Ascension, but all the butterflies appear to be tolerably numerous as individuals. Far to the south, and 1550 miles west of the Cape of Good Hope, lies the storm-swept group of Tristan da Cunha and its satellite islands, where Dr. von Willemoes Suhm of the "Challenger" found "the larvae of a *Vanessa*," probably that of *Pyrameis cardui*, which was taken there many years afterwards by Mr. de la Garde; and from the report of the two observant German seal-hunters who were found at Inaccessible Island by the "Challenger," von Willemoes Suhm concluded that there were two butterflies, a *Vanessa* and an *Argynnis*, in that island. When Diego Alvarez or Gough Island, 280 miles south of the Tristan group, was visited by the naturalists of the "Scotia" in 1904, they found "a number of beetles, and several kinds of flies," but apparently no butterfly was present. The last Atlantic island to which I shall allude is South Trinidad, 500 miles distant from Brazil. This remote speck of land, perhaps the weirdest spot on the face of the earth, was visited in 1905 by the Earl of Crawford's yacht "Valhalla," and by the "Terra Nova" in 1912, but no butterflies were seen by the naturalists in either ship, though Mr. E. G. B. Meade-Waldo, in the "Valhalla," found a few species of moths of American type.

In recent years the Fauna and Flora of the numerous small islands scattered over the Indian Ocean have been investigated by successive scientific expeditions in a fairly exhaustive manner, and we now possess a tolerably complete knowledge of their insect productions. I purposely omit any reference to the Comoro Islands, Mauritius, and Bourbon (which may be regarded as satellites to the almost continental island of Madagascar) except to recall to mind the very valuable paper by the late Colonel Manders on the butterflies of the two latter islands, which appeared in our Transactions for 1907. The eleven species recorded from Rodriguez, 300 miles east of Mauritius, are all found commonly in that island and in Bourbon. From the lofty and luxuriantly wooded Seychelles group, which are exceptional among oceanic islands from their granitic formation, twenty-two species of butterflies have been recorded, six of these being, however, somewhat doubtful. These include one *Papilio*, a dwarf form (*nana*, Obth.) of the Mascarene *P. disparilis*, Boisd.; and the handsome and peculiar *Euploea* (*Pramasa*) *mitra*, Moore, and *Atella philiberti*, Joannis, are confined to the Seychelles and to the great atoll of Aldabra, a long way to the south-west. This latter island is the sole locality of a very fine and distinct species of the characteristic African genus *Teracolus* (*aldabrensis*, Holland). The coralline Almirantes have apparently only three butterflies, a small *Pamphila* also found in the Seychelles, and two well-known European "blues," *Zizera lysimon*, Hübn., and *Tarucus telicanus*, Hübn., both also plentiful in the Mascarene Islands. On Glorioso atoll Mr. M. J. Nicoll in the "Valhalla" found butterflies and a day-flying Sphingid in numbers, one of the former being *Hypolimnas misippus*; and in the Chagos group Dr. G. C. Bourne met with the widely ranging *Precis villida*, F., and a very fine and well-marked race of *Hypolimnas bolina*, L. Only two butterflies, also of the most extended distribution, *Limnas chrysippus* and *Pyrameis cardui*, are recorded from the great coral archipelago of the Maldives. The little Cocos-Keeling atoll has produced five species, two of which, *Precis villida* and *Limnas chrysippus* var. *petilia*, Stoll, were observed by me in my flying visit to the island in January 1904. The other three are *Hypolimnas misippus*, *H. bolina*, and *Pyrameis* *cardui* var. *kershawii*, McCoy; and the predominance of the Australian element in the scanty butterfly-fauna of this little island, 1000 miles at least from the nearest point of Australia is very remarkable. Christmas Island, which consists mainly of coralline limestone upheaved to an elevation of more than 1000 feet in its highest part, possesses nine butterflies in spite of its very small area. Three of these, besides a local race (*determinata*, Butl.) of *Melanitis leda*, L., are very distinct and peculiar to the island, viz. *Euploea* (*Vadebra*) *macleari*, Butl., *Terias amplexa*, Butl., and the fine *Charaxes andrewsi*, Butl. The occurrence of the Australian form of *Limnas chrysippus* in Christmas Island is also noteworthy, as it is only 190 miles south of Java, though separated by very deep sea from this island.

The remaining islands in the South Indian Ocean, Marion, the Crozets, Kerguelen, Heard, St. Paul, and Amsterdam, all lie in a tract of the ocean too stormy and inclement for any butterfly life to be possible; and indeed they present the spectacle of a Lepidopterous fauna reduced to its lowest terms. Kerguelen, despite its area of over 1400 square miles, in a latitude nearly corresponding with that of Paris, has only two practically apterous Tineids, a third species, also apterous, having been found in the Crozets; while from St. Paul and Amsterdam, in a somewhat lower latitude, two other moths of the same family, both fully winged, have been recorded. One of these, *Blabophanes ptilophaga*, Enderlein, lives in the nests of penguins at St. Paul and feeds in the larva state on feathers; and it is a curious coincidence, to say the least, that Darwin noted at St. Paul's Rocks in the Atlantic "a small brown moth, belonging to a genus that feeds on feathers," as the sole Lepidopterous resident of that tiny islet in mid-ocean.

For our present purpose New Zealand may be regarded as an oceanic island on a grand scale, and its limited butterfly-fauna is one of the most interesting in the whole world. Of its fourteen resident species, nine are absolutely peculiar, and of these the most conspicuous, as well as perhaps the most plentiful, is the beautiful *Pyrameis gonerilla*, F., which recalls our *P. atalanta* in its appearance and its familiar habits. There are four very remarkable *Satyridae*, of which *Perenodaimon pluto*, Fereday, and *Erebiola butleri*, Fered., are mountain insects confined to the South Island, which in structure and habits exhibit a great affinity with the Erebias of the Palaearctic Region. *Dodonidia helmsi*, Fered., is a very beautiful insect having something of the facies of an Erycinid, and is found sparingly in the wooded regions on both sides of Cook's Strait; and the curious *Argyrophenga antipodum*, Doubl., which probably has its nearest allies in some of the Chilian *Satyridae*, is the characteristic butterfly of the "tussock-grass" country which covers so large an area of New Zealand, especially in the South Island. Two species of *Chrysophanus*, *salustius*, F., and *enysii*, Butl., recall our "Small Copper," and are generally plentiful, while a third species, *C. boldenarum*, White, which is more local than these, reminds one of the European *C. amphidamas* in appearance. A little "Blue," *Lycaena oxleyi*, Feld., completes the list of endemic species. Four others, characteristic of the Australian region, *Precis villida*, *Pyrameis cardui* var. *kershawii*, *P. itea*, F., and *Lycaena phoebe*, Murray, occur more or less commonly, and *Danaida plexippus*, which may have reached New Zealand as long ago as 1840, appears only sporadically, and its permanent tenure in the islands seems to be by no means secure. *Hypolimnas bolina*, *Catopsilia catilla*, Cr., and an *Euploea*, have sometimes wandered hither from their tropical home, and even our *Pyrameis atalanta*, whose nearest authentic locality is 4000 miles distant in the Hawaiian Islands, has on more than one occasion found its way to the shores of New Zealand.

In the Chatham Islands, 400 miles eastward from Cook's Strait, *Pyrameis gonerilla* has developed a well-marked race (*ada*, Alfk.), but I have no record of any other butterfly from thence. Norfolk Island, 450 miles north-west of New Zealand, has five species, the fine *Papilio amphiaraus*, Feld., allied to *P. amyntor*, Boisd., from New Caledonia, being peculiar to the island; the others being well-known Australian forms, with the exception of *Danaida plexippus*. Lord Howe Island is only six square miles in area, and is separated from the coast of New South Wales by 300 miles of deep ocean; but from this small island Mr. G. A. Waterhouse has recorded no fewer than seventeen butterflies, including such conspicuous forms as *Papilio erechtheus*, Don., and *macleayanus*, *Charaxes sempronius*, F., *Hypolimnas bolina*, etc. No butterfly has been observed as yet in the so-called Sub-Antarctic Islands of New Zealand—the Auckland, Campbell, Antipodes, and Macquarie groups—though it is just possible that in the first-named islands, which possess a rich and varied Flora of surpassing interest, one or more indigenous species may be found. This is at any rate the opinion of Mr. G. V. Hudson, who visited the Auckland Islands in November 1906, and who writes as follows: "No butterfly was seen on the islands . . . but it would be an unwarranted assumption that no butterfly exists there . . . I consider that the existence of a Satyrid butterfly on Auckland Island allied to *Erebia* or *Argyrophenga* is probable, but I do not think it likely that any member of the genus *Vanessa* occurs there . . . I always kept a very sharp look-out for butterflies, but none were seen, although on several occasions the weather-conditions for their appearance were highly favourable."

We commence our survey of the islands of the tropical Pacific with the Ladrones, from which, as far as I can ascertain, only four butterflies have been definitely recorded, these being an endemic *Atella* (*egestina*, Godt.), *Danaida plexippus*, and two species of *Euploca*; one of these, *E.* (*Nipara*) *eleutho*, Q. et G., being represented throughout Polynesia by several well-defined races. From the widely scattered Caroline Islands, some at least of which are elevated and bear a most luxuriant vegetation, Semper records a fairly rich butterfly fauna of twenty-three species, nearly all of well-known Indo-Australian forms, and including two *Papilios*, *alphenor*, Cr., and *agamemnon*, L. Mr. G. F. Mathew has also recorded from Ponape Island, a curious dwarf race of *Melanitis leda* under the name *M. ponapensis*. *Danaida plexippus* has also found its way to the Carolines, and Pagenstecher records it from the Marshall Islands; but it has apparently been unable to establish itself on the low coral islands of the Gilbert and Ellice groups, from which the only recorded butterflies are *Euploea distincta*, Butl., and *E. eleutho*, *Precis villida*, and the fine form *rarik*, Esch., of *Hypolimnas bolina*. In the lofty and luxuriant Fiji Islands we again find butterflies in considerable variety. At least twenty resident species are known, the fine *Papilio schmeltzi*, H.-S., and *Charaxes caphontis*, Hew., with the remarkable little Satyrid *Xois sesara*, Hew., and several Euploeas and *Lycaenidae*, being found nowhere else. The *Acraeinae* have here their most easterly extension in *A. andromache*, F.; this insect may possibly reach the Samoa Islands, where we find the most eastern representative of the *Papilionidae* in *P. godeffroyi*, Semper, as well as of the *Danainae* (always excluding *Danaida plexippus*) in the small *Tirumala mellitula*, H.-S. The *Hesperidae* may also find their eastern limit in Samoa, unless a butterfly that I saw once or twice in the Marquesas Islands, but was unable to capture, may belong to that family, as I suspected at the time. *Atella bowdenia*, Butl., is a characteristic species of Samoa, and occurs also in the Tonga group, where about ten species of butterflies were collected during the visit of the "Challenger" in 1874; *Belenois java*, Sparrm., and *Terias hecabe*, L., recorded also from Tonga, are the most eastern known representatives of the *Pierinae*. The Hervey or Cook Islands were visited by me in 1883, and in Rarotonga and Aitutaki I observed, besides the universal *Danaida plexippus* and *Hypolimnas bolina*, *Diadema unicolor*, Godm., *Euploea* (*Nipara*) *unicolor*, H. H. Druce, and *Jamides walkeri*, H. H. Druce, all undescribed species at the time; also *Melanitis leda* and an *Atella*, which last I was not able to catch. Far to the south-east, at the little outlying island of Oparo or Rapa, *Danaida plexippus* was the only butterfly seen by me. In two visits to Tahiti, in April and May 1883, seven species only were collected, a very small number for an island of such luxuriance and beauty. This poverty of Tahiti in butterfly life was noted by the eminent French voyager Capt. Dumont d'Urville in the "Coquille" as long ago as 1823, and the following free translation of his observations is fully in accord with my own experience sixty years later—"The farther I advance in my walk in this country, the more I have occasion to convince myself, that the entomologist who wishes to increase his collections ought not to lose his time in the South Seas. In reality, what land appears to promise a richer harvest of insects than Tahiti? What shades, what forests, are more favourable to the development of these little beings? Every where are flowers, humid places, decaying trunks and leaves. But what is the result of these laborious walks, of the assiduous researches of the naturalist? a dozen species of *Lepidoptera*, some *Hymenoptera* and *Hemiptera*, and four or five very small *Coleoptera*. Moreover, except for three species of *Nymphalidae* of which the size, the beauty, and the number of individuals strike the eye of the traveller at every moment, he would willingly believe that these islands nourish no insects whatever —Besides, the sole observation I have to make on Borabora, is that this island has afforded me a Lepidopteron which I have not yet seen in Tahiti; at the same time I have not found again another, occurring in elevated stations near Matavai (Tahiti), where it is very rare. In both islands, a *Melitaea* near *cinxia* frequents the sides of torrents, hillsides, and solitary places; and it settles but rarely, which makes it difficult to capture." This "*Melitaea*" is evidently *Atella gaberti*, Guér., a species peculiar to the Society Islands; I met with it rather commonly in Tahiti, especially in the mountain forests, where it was almost the only butterfly to be seen, and where the brilliantly gilded pupa was sometimes to be found attached to leaves. The other butterflies I observed in the island, mostly in the low ground near the shore, were *Hypolimnas bolina*, fine, large, and abundant, *Danaida plexippus*, an *Euploea*, which Mr. H. H. Druce has named *E.* (*Nipara*) *walkeri*, the finely ocellated form of *Melanitis leda* known as *taitensis*, Feld., a small race of the wide-ranging *Lampides boeticus*, and another little Lycaenid. I did not, however, meet with the brightly coloured form *taitica* of *Precis villida*, which I was informed was at times by no means rare, and here reaches the easternmost limit of this widely spread butterfly. No records are available from the Paumotu or Low Archipelago, though *Hypolimnas* and *Euploea* may extend their range to some of these widely scattered islands. In the Marquesas, which rival Tahiti in beauty and tropical luxuriance, the universal *Danaida* and *Hypolimnas* were the only butterflies that were taken during my visit, though an *Atella*? and the problematical Hesperid previously mentioned, were seen in Nuka-hiva and O-Hiva-oa, two of the larger islands.

In Pitcairn Island, though a good many moths were taken during the day I was on shore there, not a single butterfly was seen; the inhabitants without exception declared that none were found on the island, and did not recognise any of the species that I showed them. Twenty years or more after my visit to this remote spot, Mr. M. J. Nicoll, in the "Valhalla," had the same experience. He remarks ("Three Voyages of a Naturalist," p. 213)—"We saw no butterflies, but there were many small moths, and one species, *Plutella maculipennis*" (which I also noticed on Pitcairn) "was most abundant." The apparent absence of *Hypolimnas bolina* from this beautiful and fertile little island is the more remarkable, as I saw plenty of the Malvaceous undershrub which is the ordinary food-plant of the larva growing there; and the Natural History Museum at South Kensington possesses several specimens of the butterfly from the desolate Elizabeth or Henderson Island, more than 100 miles to the eastward. It has even probably reached the most remote outlier of Polynesia, Easter Island, as a butterfly, captured by Mr. and Mrs. Scoresby Routledge during their visit to that most interesting spot in 1914, can be only that species from their description of the insect, and was entirely unknown to the natives. Unfortunately the single specimen was lost during transmission home. From Caroline Island, a small atoll nearly 500 miles north of Tahiti, the Eclipse expedition of 1883 have recorded *Melanitis leda*, form *taitensis*, and *Hypolimnas bolina*, form *holdeni*, Butl.

Little or nothing is known of the insects of the other small coral islands in the equatorial region of the Pacific, but when we come to the large and lofty islands of Hawaii and its satellites, we find a fairly rich, varied, and isolated Flora and Fauna of the highest interest, which are now almost as well known as those of any region of equal extent in the Tropics. Including our *Pieris rapae*, which has been accidentally brought over from North America, and is now common and sometimes destructive, and two American Lycaenids purposely introduced in order to cope with the plague of that universal tropical shrub *Lantana camara*, the Hawaiian butterflies number nine only. Two of these are endemic species, *Pyrameis tammeamea*, Esch., by far the grandest development of the Vanessid type, and the little

Holochila blackburni, Tuely, so curiously suggestive in its coloration of a mixture of our "Purple" and "Green" Hairstreaks. *Lampides boeticus*, which is common and occurs up to 6000 feet elevation, is probably truly indigenous also, while *Danaida plexippus*, *Pyrameis atalanta*, and *P. huntera*, L., represent the American element of the fauna, and *P. cardui*, which according to Dr. R. C. L. Perkins frequently shows a strong tendency towards the form (*kershawii*) characteristic of Australia, may have been derived from that region. Neither of the two predominant butterflies of the Indo-Pacific region, *Hypolimnas bolina* and *Precis villida*, appear to have reached the Hawaiian Islands up to the present date.

Crossing to the American side of the Pacific Ocean, Clarion Island in the little-visited Revillagigedo group, south of Lower California and separated by 300 miles of deep sea from the mainland, has produced three butterflies, two small *Lycaenidae* and a sub-species of *Papilio troilus*, L. The Galapagos Islands, situated on the Equator 700 miles from the nearest point of South America, are very poor in insect life, though their fauna is otherwise of classical interest. The six known butterflies are all of American type; two of them, *Lycaena parrhasioides*, Wallgr., and *Eudamus galapagensis*, Williams, are peculiar to the islands, and the others are *Callidryas eubule*, L., *Agraulis vanillae*, L., *Pyrameis huntera*, L., and *P. carye*, Hübn. *C. eubule* and *A. vanillae* in the Galapagos are strikingly modified in the direction of small size and dark suffused coloration, being in fact well-marked races of these species. The romantic island of Juan Fernandez, 350 miles from the coast of Chile, is the last that we shall encounter in our circuit of the oceans, and *Pyrameis carye*, Hübn., which I found there in March 1882, appears to be its sole butterfly inhabitant.

We have already seen that the range of butterflies north and south is fully equal to that of flowering plants, and there is little doubt, given continuous land extending as far, that flowers and their attendant insects would be found at the North Pole itself. As it is, we find butterflies of several species maintaining their existence beyond the 80th parallel of latitude under the most rigorous conditions of climate, requiring at least two or three of the brief Hyperborean summers to complete their transformations, and apparently as much exposed to the attacks of the usual enemies of their tribe as in far more genial regions. The large proportion of Lepidopterous larvae in the Far North that are infested with Hymenopterous and Dipterous parasites has been specially noted by more than one observer; and the wariness and rapid flight of the perfect insects, not less than their beautifully protective coloration in repose, indicate with equal certainty the presence of active enemies in this state. It is not easy to say, however, what these enemies can be, unless the numerous small wading birds, and such true land birds as the snow-bunting that occur in the highest North, have developed a taste for butterflies; but on this point observations are almost or quite wanting. Many of these boreal forms have an exceedingly wide distribution; some of the species of *Colias*, *Erebia*, *Oeneis*, and *Brenthis* have been found at all points round the Polar Basin where collections have been made, and representatives of the first and last of these genera reappear at the limits of butterfly life in the Southern Hemisphere. The genus *Brenthis* in particular has the enormous range in latitude of 137°—from 81° 52′ N. to 55° 30′ S.—though with a wide break in the warmer parts of America; and the range of *Colias*, which is continued through the Tropics by the closely allied *Meganostoma*, the genus itself reappearing at high elevations under the Equator, falls short of this by only two degrees of latitude at most. In Southern Patagonia, too, we find a single species of the characteristic Arctic genus *Oeneis*.

Six butterflies stand out as pre-eminently insular forms, these being *Danaida plexippus*, *Melanitis leda*, *Pyrameis cardui*, *Precis villida*, *Hypolimnas bolina*, and *Lampides boeticus*. The range of each of these species covers an enormous area of the earth's surface, and in several cases extends to the smallest and most remote islands in mid-ocean. With regard to *Danaida plexippus*, in the "Entomologist's Monthly Magazine" for 1914 I have discussed in some detail its wanderings to our own shores, and to lands more than half the earth's circumference distant from its American home, so this most interesting butterfly will not require further consideration at present. The various geographical races (or sub-species) of *Melanitis leda* are found over a vast area in the tropical regions of the Old World, and throughout the Pacific islands to Tahiti, but apparently it has not yet reached the Marquesas or the Hawaiian groups. *Pyrameis cardui*, whose migratory habits are so well known, is perhaps the most widely distributed butterfly in the whole world, the only continent from which it is entirely absent being South America, where it is replaced by the closely allied *P. carye*, Hubn. In the Old World it ranges from Arctic Lapland and Siberia to the Cape of Good Hope, and is to be met with in the most desert as well as in the most fertile regions; it has established itself in the remotest islands of the Atlantic, except those, which like Fernando Noronha and South Trinidad, are satellites of South America; and in the Indian Ocean we meet with it even in the Maldive atolls. In the Australian region the distribution of its form *kershawii*, McCoy, extends all over Australia and to New Zealand, the New Hebrides, and New Caledonia, the Loyalty Islands being the most eastern locality in which it has been observed by me; and the same form reappears far to the north-east in the Hawaiian Islands.

Precis villida, which under the name of "Albin's Hampstead Eye," has in some unaccountable manner figured as a British butterfly in the works of our older entomologists, has a wide distribution in the Indo-Pacific region from the Chagos atoll to Tahiti, and from the Caroline Islands to New Zealand; becoming more highly coloured as we go eastward, and its brightest form (*taitica*, Feld.) is found in Samoa and the Society Islands. *Lampides boeticus* has a wider range than any other member of its great family, as it occurs in all the warmer regions of Europe and Asia, throughout Africa, the Malay Archipelago, and Australia. In mid-Atlantic it has reached Ascension and St. Helena, and the Mascarene and Seychelles Islands in the Indian Ocean; and in the Pacific I have found it in the New Hebrides, New Caledonia, and Tahiti, while Dr. Perkins records it as common in the Hawaiian Islands. It is possible that human agency has been a factor in the wide distribution of *L. boeticus*, as its larva feeds on the unripe seeds of cultivated as well as wild leguminous plants, and in some localities, as in Mauritius, it does great damage to garden peas.

I have purposely left *Hypolimnas bolina* to the last, as it is certainly the most interesting of all insular butterflies, and in its wandering propensities and adaptability to new localities, it rivals even the more famous *Danaida plexippus*. In the Indian Ocean its range has quite recently extended to Madagascar, where previous to 1915 it was quite unknown, but since that year the Oxford University Museum has received a good many specimens (of the Indian type) taken on the east coast of that great island by the Ven. Archdeacon (now Bishop) Kestell-Cornish. It probably occurs on nearly every island within the Tropics in the Pacific, with the exception, already noted, of the Hawaiian group; and it is evidently able to adapt itself to the conditions of the smallest and least fertile atolls, where even *Danaida plexippus* fails to establish a footing. Throughout its vast range the male is singularly constant in appearance, and varies only in size, in the amount of white scaling in the centre of the blue spots of both wings, and in the greater or less distinctness of the underside markings, and the subterminal series of white dots above. These dots are very conspicuous in specimens from the Indian region and from the northern and western area of its range, but as we proceed eastward, they become less distinct and finally disappear. The female, on the contrary, is perhaps the most variable of all butterflies, and nearly every fairly extensive group of islands appears to produce its distinctive race. Specific rank has been accorded by various Lepidopterists to many of these forms, but it seems to me nearer the truth to regard them as variations of a single polymorphic species, resulting from different conditions of environment, rainfall, temperature and other modifying influences.

The form of *H. bolina* found by Dr. G. C. Bourne in Diego Garcia (Chagos Islands) is specially remarkable for the great extension of the white markings above and beneath, and a closely similar variation has, curiously enough, been observed in Palawan Island in the Philippines. It is in the Fiji Islands that the variation of the butterfly probably reaches its maximum; the female there ranges from a practically unicolorous fulvous, pale ochreous, or even whitish-ochreous ground-colour in which the distinctive markings are nearly lost, to the large and handsomely marked form *nerina*, F., of Queensland, the

New Hebrides, and New Caledonia, and the still more richly coloured *pulchra*, Butl., of the latter island, and *rarik*, Esch., of the scattered groups to the northward. Nearly all the specimens that I have seen from the Friendly Islands (Tonga) are, on the contrary, smaller and more poorly marked than those from any other locality, but those that I bred from larvae found in Rarotonga and Aitutaki are very handsome, and the females are for the most part intermediate between the fulvous Fijian form and the large dark race occurring in Tahiti. The markings of the females from the Society Islands approximate more nearly to those of the male than is the case with any that I met with elsewhere, except in the Marquesas, where the local race of *H. bolina* differs from that of Tahiti chiefly in its smaller average size and somewhat darker general colouring.

The above instances convey only a faint idea of the marvellous range of variation in the female of this most interesting butterfly, which can be realised only by the inspection of the extensive series from the whole of the area of its distribution, contained in the National Collection, or the almost equally fine series in the Oxford University Museum.

It is not my intention at present to discuss the means by which butterflies have been dispersed over the oceans to the most remote islands, especially as this subject has been treated somewhat fully by me in the case of *Danaida plexippus*, in the volume of the "Entomologist's Monthly Magazine" for 1914. The brief bibliography and sketch-map appended to this Address will, I trust, enable any one who is interested in the geographical distribution of butterflies, to follow these frail creatures to their ultimate limits on the earth's surface, and to travel in imagination to the Fringes of Butterfly Life.

BIBLIOGRAPHY.

ARCTIC.

1823. Scoresby, William, junr. Journal of a Voyage to the Northern Whale Fishery, p. 204. Appendix V, Insecta, by Prof. Jameson, Edinburgh.

1835. Curtis, J. Appendix to the Narrative of a Second Voyage in search of a North-West Passage, by Sir John Ross, 1829–33, pp. lxv–lxx, t. A.

1867. Hayes, I. I. The Open Polar Sea, pp. 412, 433.

1874. Hartwig, G. The Polar World, pp. 248–51 (translation of extract from Middendorff's "Siberische Reise," 1844–5).

1877. McLachlan, R. Report on the Insects . . . collected by Capt. Feilden and Mr. Hart between the parallels of 78° N., and 83° N., during the recent Arctic Expedition. Proc. Linn. Soc. Lond., xiv, pp. 108–9.

1881. Markham, A. H. A Polar Reconnaissance, p. 234.

1886. Aurivillius, Chr. Lepidopteren insamlade i nordligaste Asien under Vega Expeditionen. In Vega Exp. Vetensk. iakttageler, ser. iv, pp. 73–80.

1886. Greeley, A. W. Three Years of Arctic Service, vol. i, pp. 372, 385.

1898. Peary, R. E. Northward over the "Great Ice," vol. i, p. 352.

1900. Aurivillius, Chr. Lep. och Coleop. insamlade under Prof. A. G. Nathorst's arktiska expeditioner . . . 1898 och 1899. Öfv. Kongl. Vetensk.-Akad. Förh., lvii, pp. 1135–44.

1903. Elwes, H. J. On a Collection of Lepidoptera from Arctic America. Trans. Ent. Soc. Lond., 1903, pp. 239–43, pl. ix.

1906. Poppius, B. Beiträge zu Kenntnis der Lepidopteren Fauna der Halbinsel Kanin. Helsingfors; Acta Soc. Fauna Fl. Fenn., 28, No. 3, 1906, pp. 1–11, pl. i.

1906. Rowland-Brown, H. Some Notes on Scandinavian and Lapland Butterflies. Entom., vol. xxxix, pp. 242–7, pls. vii, viii.

1910. Johansen, F. Danmarks Expedition, N. E. Greenland, Medd. og Grønland, xliii, pp. 50, 51.

1912–13. Sheldon, W. G. The Lepidoptera of the Norwegian Provinces of Odalen and Finmark. Entom., vol. xlv, pp. 309–15, 337–46, pl. xii–xiv; vol. xlvi, pp. 11–15.

SOUTHERN.

1877. Berg, C. Beiträge zu den Lepidopteren Patagoniens. Bull. Soc. Imp. Nat. Mosc., lii, 2, pp. 1–22.

1881. Walker, J. J. Entomological collecting on a Voyage to the Pacific. Ent. Mo. Mag. vol. xviii, pp. 82–3.

1887–9. Trimen, R. South African Butterflies.

1891. Mabille, P. Mission Scientifique du Cap Horn, 1882–3, vi, div. 2–3, pl.

1903. Vallentin, R. Notes on the Falkland Islands. Mem. and Procs. of the Manchester Lit. and Phil. Soc., xlviii, No. 23, pp. 21–22.

1911. Waterhouse, G. A., and Lyell, G. The Butterflies of Australia.

INSULAR.

Atlantic Ocean.

1870. Godman, F. D. The Natural History of the Azores or Western Islands. Lepidoptera, pp. 101–3.

1879. Moseley, H. N. Notes by a Naturalist in the "Challenger," p. 134.

1879. Wollaston, E. The Lepidoptera of St. Helena. Ann. Mag. Nat. Hist. (5), iii, pp. 221–4.

1894. Ridley, H. N. Notes on the Zoology of Fernando Noronha. Journ. Linn. Soc. Zool., xx, p. 543.

1895. Garde, P. de la. African Rhopalocera. Entom., xxviii, pp. 153–5.

1901–2. Verrill, A. E. The Bermuda Islands. . . . Trans. Connecticut Acad., xi, part ii, pp. 756–66.

1908. Nicoll, M. J. Three Voyages of a Naturalist (for S. Trinidad I.).

Indian Ocean.

1879. Butler, A. G. Zoology of Rodriguez. Lepidoptera. Phil. Trans., clxviii, pp. 541–2.

1886. Bourne, G. C. General Observations on the Fauna of Diego Garcia, Chagos Group. P.Z.S., 1886, p. 333.

1900. Butler, A. G. Monograph of Christmas Island. Insecta, pp. 60–63.

1907. Manders, N. The Butterflies of Bourbon and Mauritius. Trans. Ent. Soc. Lond., 1907, pp. 429–54.

1909. Jones, F. Wood. The Fauna of the Cocos-Keeling Atoll. (Lepidoptera). P.Z.S. 1909, pp. 144–5.

1909. Fletcher, T. B. Lepidoptera (exclusive of the Tortricina and Tineina) . . . (of) the Indian Ocean. Report of the Percy Sladen Trust Expedition. Trans. Linn. Soc. Lond., ser. ii, vol. xiii (Zoology), pp. 288–96, and table, p. 315.

Pacific Ocean.

1832. Dumont d'Urville, J. Voyage de l'Astrolabe pendant les années 1826–9. Faune entomologique de l'Océan Pacifique, par le Dr. Boisduval. I. Lépidoptères, pp. 20–2.

1874. Butler, A. G. List of the Diurnal Lepidoptera of the South Sea Islands. P.Z.S., 1874, pp. 274–91.

1883. Butler, A. G. The Lepidoptera collected during the recent expedition of H.M.S. "Challenger" (for Friendly Islands). Ann. Mag. Nat. Hist. (5), xi, pp. 402–4.

1883. Walker, J. J. Entomological Collecting on a Voyage in the Pacific. Ent. Mo. Mag., xx, pp. 91–6, 222–3.

1884. Butler, A. G. On a Collection of Butterflies from the Fiji Islands. Ann. Mag. Nat. Hist. (5), xiii, pp. 243–348.

1885. Butler, A. G. Lepidoptera collected by Mr. C. M. Woodford in the Ellice and Gilbert Islands. Ann. Mag. Nat. Hist. (5), xv, pp. 238–42.

1888. Olliff, A. S. Report on a small Zoological collection from Norfolk Island. Proc. Linn. Soc. N. S. Wales, ii, vol. ii, Insects, pp. 1013–14.

1890. Druce, H. H. Descriptions of two new species of *Euploea* from the South Sea Islands. Ent. Mo. Mag., xxvi, p. 320.

1897. Waterhouse, G. A. The Rhopalocera of Lord Howe Island. Proc. Linn. Soc. N. S. Wales, vol. xxii, pp. 285–7.

1898. Hudson, G. V. New Zealand Moths and Butterflies, pp. 101–21.

1899. Meyrick, E. W. Fauna Hawaiiensis. I. Macrolepidoptera, pp. 193–5.

1904. Waterhouse, G. A. On three Collections of Rhopalocera from Fiji, and one from Samoa. Trans. Ent. Soc. Lond., 1904, pp. 491–5.

1906. Semper, G. Beitrag zur Lepidopterenfauna des Karolinen Archipels. D. Ent. Zeits. Iris., Berlin (18) 1906, pp. 245–67.

1909. Hudson, G. V. The Subantarctic Islands of New Zealand. II. General Notes on the Entomology of the Southern Islands of New Zealand, pp. 59–60.

1909. Pagenstecher, A. Die geographische Verbreitung der Schmetterlinge.

1912. Williams, F. X. The Butterflies and Hawk-moths of the Galapagos Islands. Proc. Calif. Acad. Sci. (ser. 4), i, 1911, pp. 289–322, pls. xx, xxi.

1913. Perkins, R. C. L. Fauna Hawaiiensis, Introduction, pp. cliv–clvi.

1914. Walker, J. J. The Geographical Distribution of *Danaida plexippus*, L. (*Danais archippus*, F.), with especial reference to its recent migrations. Ent. Mo. Malg., l, pp. 181–93, 224–37.

1919. Routledge, Mrs. Scoresby. The Mystery of Easter Island, p. 152.

THE PRESIDENT'S ADDRESS

LADIES AND GENTLEMEN,

The session which terminates with this evening's Meeting has undoubtedly been one of the most eventful in the whole history of the Society. In the first place, mainly owing to the generous response of a large body of our Fellows to the appeal for the funds necessary to carry out the undertaking, and to the energetic efforts of our indefatigable Treasurer, we have at last been able to secure as our own property a home which we trust will be worthy of the traditions and dignity of the most influential association of Entomologists in existence. Our new home will be shared with us, for some years in any case, by the Imperial Bureau of Entomology, and thus its importance and utility as the head-quarters of our Science in the British Empire will be enhanced in no small measure. Moreover, our new and ample accommodation will enable the treasures of our Library to be displayed to far greater advantage, and to be rendered much more accessible and available to our Fellows, than they have been for so many years in the cramped and congested space they have of necessity occupied. We deeply regret, however, that the valuable services of Mr. G. C. Champion, our Honorary Librarian for the last thirty years, are no longer available to us. During the long period in which he has held this office, his unfailing attention to its arduous and responsible duties, and the conspicuous ability with which these duties have been performed, have earned for him the unfeigned gratitude of the Society as a body; and it must not be forgotten that to him we owe the first printed catalogue of our great collection of Entomological works, as well as its

"Supplement," issued a few years afterwards. In our new Honorary Librarian, Mr. H. J. Turner, I am convinced that we shall find a worthy successor to Mr. Champion in this important office.

The acquisition of our new premises has not been free from difficulties, legal and otherwise; and we are greatly indebted to our Fellow, Mr. W. G. F. Nelson, for his most kind and valuable advice and assistance in enabling us to surmount these obstacles. The preparations for the occupation of our new home proceed apace, and we assemble this evening for almost, if not quite, the last time in the room in which, ever since the year 1874, our meetings have been held. It is only fitting here to acknowledge the cordial relations that have subsisted between the Medical Society of London and ourselves, during the long period of our tenancy of their rooms.

In common with all other scientific Societies, we have felt severely the pinch of the present hard times, and it has been found imperatively necessary to increase our Entrance Fee and Annual Subscription very materially. This increase, however, has not prevented the addition to our ranks of an unprecedented number of new Fellows, and our losses by resignation and by death have been more than made good. The cost of paper, of printing, and especially of every form of illustration, instead of becoming less as we hoped last year, continues ever to increase, and is now almost prohibitive; our Transactions have in consequence suffered somewhat, and though the quality of their contents remains as high as ever, they are smaller in bulk than has been the case for many years past, and it has been necessary to defer the publication of several important papers.

During the past year we have lost by death thirteen of our colleagues, including our senior Fellow, the Rev. Henry S. Gorham, who joined the Society as long ago as 1855. He possessed an intimate knowledge of British and exotic Coleoptera, and his Entomological writings, all of which deal with this Order of Insects, extend over a period of forty years. Among these the most important are the "Endomycici Recitati," published in 1873, and his contributions to the "Biologia Centrali-Americana," in which great work he was responsible for the *Malacodermata, Erotylidae, Endomychidae* and *Coccinellidae*. Another veteran who has gone from among us, although he was rarely seen at our meetings, is Mr. Alfred E. Hudd of Bristol, an accomplished antiquarian as well as Entomologist, whose election to the Society dates from 1865. By the untimely death of Mr. Frank Milburn Howlett the Society has been deprived of an Entomologist of great acquirements and even greater promise, especially in the biological and physiological aspects of our Science; and the same may be said of the late Dr. Charles Gordon Hewitt, the Dominion Entomologist of Canada, whose work was on closely similar lines. Another serious loss is that of Prof. Leonard Doncaster, F.R.S., whose researches in the field of genetics mark an era in biological science; and in particular his discovery in 1906 of the phenomena of sex-determination in *Abraxas grossulariata*, as the result of an elaborate series of breeding experiments, is of the greatest interest to Mendelians. The death within the last few days of Dr. H. H. Corbett and Mr. J. W. Carter deprives Yorkshire of two of its most prominent Entomological workers; two well-known Dipterists have passed away in the Marchese Piero Bargagli and Mr. Frederick C. Adams; and Australia has lost her premier Arachnologist in Mr. William J. Rainbow, the Entomologist to the Australian Museum, Sydney, whose death took place in November 1919. To these may be added the names of Commander the Hon. Richard O'B. Bridgeman, R.N., F. M. Campbell, and James T. McDougall, respecting whom, however, I have no particulars; nor must we omit the names of Frederick Herschel Waterhouse, the last survivor of a family of distinguished Entomologists, and of William West, known to most of us as a frequent visitor and exhibitor at our meetings for many years past, although neither was a Fellow of the Society.

I now proceed to the Entomological essay which custom requires of the President on these annual occasions.

SOME ASPECTS OF INSECT LIFE IN NEW ZEALAND.

The choice of the subject of my Address has been determined by two considerations. First of all, nearly twenty years ago, during my last commission abroad in H.M.S. "Ringarooma," it was my good fortune to spend more than a year in New Zealand waters; to make the acquaintance of many able and enthusiastic entomologists in the Dominion; to consult most of the principal collections of New Zealand insects in the Museums and in private hands; and to carry away with me some of the most pleasant memories of my life, gained in acquiring first-hand experience of these insects in the field. Secondly, this experience has enabled me fully to realise the extreme interest and importance of the entire New Zealand fauna, and the fascinating field of research and speculation as to its origin and affinities, which it presents to the student of the geographical distribution of animal life. On some of these problems I propose to touch, however lightly, in the course of this Address, which in addition may have some little value as a summary of our knowledge of the Entomology of New Zealand, brought up as nearly as possible to the present date.

It has become a common custom to speak of New Zealand as the "Britain of the South," but it would be difficult to find two regions, nearly equal in area and both in the Temperate Zone, more utterly diverse in physical and faunistic conditions. The British Islands are essentially a part of the great Euro-Asiatic continent, from which they were separated as it were yesterday in geological time; and their insect fauna is but a greatly reduced edition of that of Europe, and includes only a very limited number of species which may be regarded as peculiar. New Zealand, on the contrary, has almost certainly not been directly connected with any of the great land-masses since the commencement of the Tertiary period at latest, and it possesses in consequence the most isolated and precinctive fauna of any region in the whole world. From Australia, the nearest land which may be regarded as a continent, the islands are separated by the Tasman Sea, an extent of more than a thousand miles of storm-swept and profoundly deep ocean, and the coast of South America is at least four times as far away across the Pacific. Southwards, a vast expanse of deep ocean, broken only by one or two groups of small islands, extends to the eternal ice of the Antarctic

Continent; and only to the northward do we find evidence of a former connection with other regions, in the submarine plateau included within the thousand-fathom line of soundings which surrounds New Zealand and its satellite islands, extending nearly as far as New Caledonia, and probably indicating the limits of an ancient continent of which these islands are the sole relics at the present day.

New Zealand may on the whole be regarded as an eminently diversified and mountainous land, its highest summit, Mount Cook (Aorangi) in the Southern Alps, attaining an elevation of 12,347 feet; and as the Islands extend over fourteen degrees of latitude, from 34° 25′ to 47° 20′ S., almost every variety of climate except that of the Tropics may be found within their limits. The rainfall varies from about 25 inches per annum in the drier parts of the South Island, to as much as 150 inches in the Sounds on the south-west coast, which are exposed to the full force of the prevailing westerly winds of those latitudes; and with the usually moderate range of temperature, and the general abundance of sunshine, the conditions throughout the Islands are favourable to vegetable life in an eminent degree. The first European visitors found the whole country, except on the higher slopes of the mountains and a few limited lowland tracts, covered with dense forest, which in the dimensions of its individual trees, the luxuriance of the undergrowth, and the profusion of epiphytes, climbing plants and especially of ferns of endless variety and of all sizes, was probably unsurpassed in picturesque beauty and botanical interest anywhere in the Temperate Zone. But over a great area of both Islands this noble forest is but a memory, and has vanished before the axe of the "timber-getter," and even more through the indiscriminate use of fire for clearing the country for agricultural and grazing purposes. In many districts all that remains to tell of its former glories is an occasional decaying log or tree-fern stump on a bare hillside, or a hideous array of miles of charred trunks of once majestic trees, rising from a tangled growth of furze, sweetbriar, and blackberry bramble, more impenetrable than the original "bush" and much more difficult to deal with. In the immediate vicinity of some of the principal towns, notably at Nelson and Christchurch in the South Island, one may walk for a long distance without seeing a single indigenous plant, so completely has the native flora been ousted by introduced trees, shrubs, and weeds, mostly from our own country. No fewer than 350 species of these intruders were a few years ago enumerated by Mr. T. F. Cheeseman as having become more or less established in the neighbourhood of Auckland,* and many of these weeds grow with a vigour and luxuriance quite unknown in their native land. The disastrous effect on all forms of life of this destruction and replacement of the original vegetation need hardly be enlarged upon, and as it continues at an even accelerated pace, the necessity is only too obvious for immediate and thorough research in what still remains of the endemic animal life of New Zealand, before many of its most interesting forms are lost for ever. Fortunately there is in the Dominion at the present time a small but exceedingly capable body of Entomologists who are fully alive to the urgency of the matter, and the number of new and interesting forms in all Orders of insects brought to light by them in recent years bears ample testimony to their successful exertions. Even near the larger towns, notably at Dunedin, where a wide belt of " bush " surrounding the city has been specially reserved, some patches of the original woodland have escaped the general destruction, and still give shelter to many interesting insects and other forms of indigenous life.

The New Zealand forest is mostly evergreen in character, and thus varies but little in aspect at different seasons of the year. In many parts, especially at low elevations, it is largely composed of four or five noble species of Coniferous trees, chief of which is the famous " Kauri," one of the most magnificent timber trees in the world, but now rapidly approaching practical extinction, and found only in the northern half of the North Island. In the less settled parts of the Dominion, and in particular on the flanks of the mountain ranges, large stretches of forest still remain practically in their primeval condition, the subalpine scrub being of an exceedingly dense and impenetrable character, but containing many fine and curious flowering shrubs, some of which are now well known in cultivation. Towards the west the prevailing trees are several species of *Nothofagus*, a very interesting group of small-leaved, mostly evergreen beeches, miscalled "birch" in New Zealand, and "myrtle" in Tasmania. Trees of this genus are also predominant in the forests of Western Tasmania and Western Patagonia, to which they impart a characteristic aspect in common with those of New Zealand; and their present-day distribution strongly suggests the common origin of these widely-dispersed trees in a long-vanished sub-Antarctic land.

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* Transactions, N.Z. Institute, XV, pp. 268–298.

Comparatively few of the trees and shrubs in the lowland forests have conspicuous flowers, with the exception of the genus *Veronica*, which here includes trees of considerable dimensions, and the Myrtaceous genus *Metrosideros*, in which are some fine timber-trees as large as English oaks, whose many-stamened crimson and pink blossoms are in their season a most beautiful and conspicuous feature of the "bush." Where not actually under cultivation, the open ground unoccupied by forest is, in the North Island, covered in great part with a dense growth of "manuka" or "tea-tree" (*Leptospermum*), a Myrtaceous shrub or small tree whose profuse and fragrant white blossoms rival those of the hawthorn in their attractiveness to insects; or with a robust variety of our bracken (*Pteris aquilina* var. *esculenta*), the rhizome of which in old times formed an important item in the food-supply of the Maoris. In the South Island are wide expanses of level or slightly undulating land, sometimes many miles in extent, and covered with tall grass growing in definite "tussocks," other vegetation being usually little in evidence. This "tussock-land," which forms the finest of pasture, extends in places far up the mountain-sides, where, above the "timber-line," an Alpine flora exceedingly rich in species, and including many of the most remarkable and beautiful plant-forms of New Zealand, is found up to the limits of perpetual snow.

The diversified surface, the favourable climatic conditions, and the luxuriant vegetation of these beautiful Islands, at once suggest the existence of a profusion of species and individuals in all Orders of insects; and in the light of our present knowledge, it is a little difficult to realise the opinion which prevailed up to quite a recent date, that New Zealand possessed probably the poorest and most limited insect fauna of any land of the same extent. Even as late as 1876, we find so eminent an authority as Mr. A. R. Wallace writing of its "excessive and most unintelligible poverty in insects,"* and further on in the same great work,† he is disposed to attribute this poverty to the deficiency of the flora in gaily-coloured and conspicuous flowers—a deficiency by no means as great as was then generally supposed. And an excellent Entomologist, the late Prof. F. W. Hutton, writes as follows in 1873—"No New Zealand naturalist who has collected insects on however small a scale in Europe can I think fail to be struck with the paucity in New Zealand, not only of species, but in some Orders of individuals also. . . . On entering the bush, instead of finding the masses of decaying wood and leaves swarming with life, we hardly find a living creature, while at the same time we are attacked by myriads of blood-thirsty mosquitos (*Culex acer*). It would certainly seem that abundance of food does not produce abundance of individuals in some Orders (e. g. *Coleoptera*), neither does an absolute dearth of food in the imago state prevent the increase of individuals in others (e. g. *Diptera*)."‡ Another good observer, Mr. C. M. Wakefield, states also at about the same time—"3000 species of Coleoptera have been found in Great Britain, and although I cannot say how many New Zealand species have been described, yet I do not think the number can possibly exceed 500. When, therefore, we consider what a diversity of climate and surface these islands present, it is obvious that there is ample scope for further investigation. Not only are our species few in number, but the individuals composing them are small and inconspicuous, and singularly destitute of brilliant colouring. The same dull and sombre hue so characteristic of the vegetation of New Zealand extends itself, with but few exceptions, to its fauna."§

The reason for this striking under-estimate of the richness of the New Zealand insect fauna is not far to seek, for it is undoubtedly due to the fact that its great interest and importance were until quite recently not realised by entomologists in general, previous to which a certain lack of superficial attractiveness in the insects as a whole had led to their being somewhat neglected by collectors, professional and otherwise. The close research and observation carried out during the past thirty years by the resident entomologists of New Zealand, with the aid of such capable visitors from England as Mr. E. Meyrick and others, have completely dissipated the idea of an insect fauna unduly poor in number of species. But these researches have emphasised the isolated and distinctive character of the fauna, by revealing the striking inequality in the representation of the different Orders of insects, and the entire absence in all, of a great number of groups otherwise of almost universal distribution. Indeed, it may be said that the interest of the New Zealand insect fauna as a whole consists almost as much in its deficiencies, as in what it includes.

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* Geog. Distribution of Animals, I, p. 450.

† Id., pp. 460–63.

‡ Trans. N.Z. Inst., V, p. 246.

§ Id., V, p. 297.

Comparatively few of the New Zealand insects are of diurnal or obtrusive habits, and their general apparent scarcity, in species at any rate, is very evident to the ordinary collector, as indeed it was at first to myself. A very large number of insects in all Orders, especially in the Coleoptera, are most efficiently protected from casual observation by their inactive and retired habits, and even more by the eminently cryptic nature of their form and colouring, which harmonise in a greater degree with their special surroundings than is probably the case with the members of any other fauna. Very many species are exceedingly local, and confined to a very small area, and a large number of the finer forms now known have been recently obtained from mountain localities more or less difficult of access. When, however, the entomologist from England has realised the peculiar conditions under which most of the endemic insects live, he will find collecting fully as pleasant and remunerative as at home, though it may call for a greater amount of acumen and perseverance.

In the neighbourhood of the larger towns, the insects introduced accidentally or of set purpose from our own country, such as the hive-bee, the humble-bees of three or four species which were imported with much difficulty some fifty years ago, and which now abound everywhere, the blow-fly *Calliphora erythrocephala* Meig., and the drone-fly *Eristalis tenax* L., intrude themselves on the notice of the entomologist much more than is the case with the endemic insects of the Islands. They are, in fact, fully as much in evidence as the swarms of sparrows, greenfinches, linnets and starlings which have everywhere replaced the far more interesting small native birds, except in the recesses of the "bush" remote from cultivation.

The history of the progress of our knowledge of the Coleopterous fauna of New Zealand is very interesting. The first small collection brought to England, which, however, included several of the largest and most conspicuous species, was made during the memorable first visit of Capt. Cook to the islands in 1769–70; and many of these insects, which were described by Fabricius, still exist in the Banksian Collection in the Natural History Museum at South Kensington. Little or nothing was added to our knowledge until 1841, when some beetles were collected at Akaroa, Port Chalmers, and the Auckland Islands by the French expedition to the South under Capt. Dumont d'Urville; and a few were also obtained at the Bay of Islands in the North Island by the naturalists of our own Antarctic ships commanded by Capt. Sir James C. Ross. These latter insects, with a few more from other entomologists, among them Charles Darwin in the "Beagle," were described by Adam White in 1846 in the "Zoology of the Voyage of H.M. Ships Erebus and Terror," about 150 species of Coleoptēra being then known from New Zealand. A small collection from the Christchurch district, sent home in 1867 by Mr. R. W. Fereday, was described in the "Entomologist's Monthly Magazine" of that year by Mr. H. W. Bates; and from this date the serious investigation of the New Zealand Coleoptera may be said to have commenced. Several valuable papers by the late Prof. Hutton, Capt. T. Broun, Mr. C. M. Wakefield, and other entomologists resident in New Zealand, as well as by Mr. F. P. Pascoe and Dr. D. Sharp, appeared between 1873 and 1884, mostly in the Transactions of the New Zealand Institute; and in 1885 the last-named eminent Coleopterist, in the Transactions of the Royal Dublin Society,* made what was up to that time by far the most important contribution to our knowledge of the New Zealand beetle-fauna, mainly based on a very large collection from the South Island received from Mr. R. Helms of Greymouth. In this fine paper, to which I am greatly indebted, Dr. Sharp estimates "that New Zealand will be found to possess somewhere between 3000 and 3500 species of Coleoptera," a prediction which has been more than fulfilled. Prior to that date, however, Captain (afterwards Major) T. Broun, whose decease we have quite recently had to deplore, had issued at Wellington in 1880 the first part of his "Manual of New Zealand Coleoptera," in which 1141 species were enumerated. This work, although in parts decidedly open to criticism, has been of very great value to every one interested in the entomology of New Zealand; and to the end of his long life the author continued, almost single-handed and under many difficulties, to describe the multitude of hitherto unknown forms brought to light by his own researches and those of the other Coleopterists resident in the Dominion. The endemic members of several important families, such as the *Byrrhidae*, the *Cossonides*, and especially the *Pselaphidae*, have been revised by him in quite recent years. Just before his lamented decease, Prof. F. W. Hutton in 1904 published his exceedingly useful "Index Faunae Novae Zealandiae," which includes a complete catalogue of the insects as known up to that date, and enumerates 2735 species of Coleoptera as occurring in the Islands. At the present time about 4000 species, a number considerably in excess of that of our British beetles, are known to inhabit the New Zealand Region, and these are comprised in nearly 700 genera.

The unequal representation of the New Zealand insects is in no Order so strikingly evident as in the Coleoptera. Thus the important families *Cetoniadae* and *Cassididae* are entirely absent from the fauna; and only four small species of the *Buprestidae*, so abundant in species and individuals in Australia, have as yet been found in New Zealand. The great group of true dung-beetles, as might indeed have been expected in the case of a region which in all probability has never supported any terrestrial Mammalia except two small species of bats, are here represented only by a very few small forms of *Saphobius* (*Copridae*) and *Ataenius* (*Aphodiidae*), which are found under bark and in vegetable refuse. The very curious little blind Aphodiid *Phycochus graniceps* Broun, which lives in the sand under half-buried logs at high-water mark on the coasts, has, singularly enough, been found under similar conditions in Tasmania, in company with another member of the genus. The *Dytiscidae* number only sixteen species, and only one of these, the rare *Homoeodytes* (*Cybister*) *hookeri* White is of large size; our familiar *Rhantus pulverosus* Steph., whose range extends from our own islands to Tongatabu in mid-Pacific, being of very common occurrence. The *Chrysomelidae* again are few in species, except perhaps in the Galerucine genus *Luperus*, and they do not present a single form of large size or striking appearance. On the other hand the *Cicindelidae*, *Hydrophilidae*, *Staphylinidae*, *Lucanidae*, *Elateridae* and *Dascillidae*, as well as the *Heteromera*, are relatively much better represented, and the Longicornes can boast of some 220 species, a large number for a temperate region, though only two of these, *Prionoplus reticularis* F. and *Ochrocydus huttoni* Pasc., both among the most conspicuous of New Zealand insects, represent the large section of the *Prioninae*. The *Carabidae*, of which, however, the first sub-family (Carabides) has for its sole exponent the very anomalous *Amarotypus edwardsi* Bates, forms one of the largest and most important elements of the Coleopterous fauna, being only exceeded in this respect by the *Curculionidae*, of which family more than a thousand species are now known from the New Zealand region. The sub-family *Cossoninae*, which is characteristic of insular insect faunae in an eminent degree, is here developed to an extent proportionately exceeded elsewhere only in the Hawaiian Islands and in St. Helena. A single tree, the Nikau (*Rhopalostylis sapida* Sol.), the sole endemic palm, supports an interesting series of some eight or ten species included in four genera, and other remarkable forms of the sub-family are restricted to the tree-ferns

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* New Series, Vol. III, pp. 351–452, plates XII, XIII.

(*Cyathea*) and to the so-called "native flax" (*Phormium tenax* Forst.). A single species of the curious genus *Rhynchogonus*, whose head-quarters are in the Hawaiian Islands, has been found in New Zealand, and another has recently been met with in the Kermadec Islands to the northward. The *Cryptorrhynchina* are also very fully represented, especially *Acalles* and the allied genera, which include some very fine endemic forms. There are five species of the small but remarkable family *Rhysodidae*, a large number for a single limited region, and one of the very few members of the very aberrant family *Aglycyderidae* (*A. wollastoni* Sharp) is found rarely on the tree-ferns, the only other two species occurring in such remote localities as New Caledonia and the Canary Islands. The *Anthribidae* also include a considerable number of interesting insects, nearly all, however, being of small size; and in the *Colydiidae* and the *Pselaphidae* especially, the industrious researches of the present school of New Zealand Coleopterists, notably among them the late Major Broun, have revealed a wealth of species probably unequalled anywhere else in the world in singularity of form and diversity of structure.

COMPARATIVE TABLE OF REPRESENTATION IN CERTAIN GROUPS OF COLEOPTERA

Family or Section.	New Zealand (4000 species).		British Islands (3420 species).		Hawaiian Islands (1107 species).		St. Helena (129 species).	
	Genera.	Species.	Genera.	Species.	Genera.	Species.	Genera.	Species.
Cicindelidae	1	19	1	5	—	—	—	—
Carabidae	55	483	70	316	36	204	1	14
Dytiscidae	7	16	18	107	—	—	—	—
Pselaphidae	23	318	13	36	—	—	—	—
Colydiidae	27	171	15	19	1	1	—	—
Lucanidae	4	35	3	3	1	7	—	—
Cerambycidae	51	224	32	55	5	52	—	—
Phytophaga	17	139	52	247	—	—	1	3
Curculionidae	193	1049	96	476	12	132	15	65
(Apionides)	1	1	1	80	—	—	—	—
(Cossonides)	51	160	7	9	13	89	13	54
Anthribidae	9	73	5	8	—	—	3	26

In this connection it may be interesting to compare the representation of some of the principal families and subfamilies of Coleoptera in New Zealand with that of the truly endemic members of the same groups in two equally precinctive and peculiar insular faunae which have been about equally investigated, and with the same groups as found in the British Islands.

The great majority of the New Zealand beetles are of moderate or quite small dimensions, and are characterised rather by endless diversity of form and sculpture than by bright or conspicuous colouring. The largest beetle of the Islands, *Prionoplus reticularis* F., slightly exceeds our *Prionus coriarius* in size, and the single representative of the *Brenthidae*, *Teramocerus* (*Lasiorrhynchus*) *barbicornis* F., of which the male is often more than three inches in total length, is one of the finest and largest of the family, as well as one of the most remarkable and conspicuous insects in the fauna of the Islands. But there are, after all, a good many exceptions to the general dullness. The large metallic-green and coppery species of *Trichosternus* and *Zacopoecilus* rival many of the European *Carabi* in size and brilliancy of colour, and another fine and very characteristic genus of the same family is *Mecodema*, of which nearly sixty species are now known from New Zealand, only two or three others occurring in Australia and Tasmania. These are black or dark bronzy beetles of varied and often elegant sculpture, the finest, *M. costellum* Broun, coming from Stephens Island in Cook's Strait, where also the largest species of the endemic Tenebrionid genus *Cilibe* is found. In the rich green flower-frequenting species of *Rygmodus* we find a brightness of colouring quite unusual in the *Hydrophilidae*, and the little " chafers " of the genus *Pyronota*, some of which are most abundant in summer on *Leptospermum* and other blossoms, yield to very few of their tribe in beauty of metallic colour. Their larger relative, the exceedingly rare *Poecilodiscus pulcher* Broun of the mountains of the South Island, is even more brilliant, and the largest Buprestid, *Nascio enysii* Broun, is also a charming little beetle. Among the *Elateridae* are some quite fine insects, one of the most singular being the large flattened *Psorochroa granulata* Broun, which is found rarely in crevices of rocks near the sea in some of the small off-lying islands; and the

Cleridae also include some very pretty little insects. Few Longicorns for their size exceed in elegance of form or beauty of subdued colour such species as *Hexatrichia pulverulenta* F., *Coptomma variegatum* F. (both of which, like *Teramocerus barbicornis*, have in recent years become very much less common than formerly), the apple-green *Calliprason sinclairi* White, and especially the little flower-frequenting members of the genus *Zorion*; while the large and rare *Blosyropus spinosus* Redt. of the South Island is one of the most quaint-looking beetles even in New Zealand. It is in the *Rhynchophora*, however, that we find the most singular and diversified forms of the endemic Coleoptera. The members of the small sub-family *Scolopterinae* (*Nyxetes*, *Ancistropterus*, *Scolopterus*, etc.) present a little assemblage of knobbed and spinose weevils of most distinctive appearance, quite unlike any forms from elsewhere, and the species of *Stephanorrhynchus*, *Hoplocneme*, and *Rhadinosomus*, to name only a few, are hardly less bizarre in aspect. Metallic or bright colours are rare in this family here, but a large number of species are of neat and attractive appearance, and the members of the genera *Rhynchodes*, *Agathinus*, *Lyperobius*, *Phaedrophilus*, and some other forms recently discovered in the mountains of the South Island at considerable elevations, are decidedly handsome insects.

Comparatively few of the beetles are individually numerous, the *Cicindelidae* forming one exception; *Cicindela tuberculata* F. in the North Island, and *C. latecincta* White in the South, are to be seen everywhere on roadsides and dry banks in summer, and are familiar to the youth of the Dominion under the curious name of "New Zealand bees." Only a few species may be regarded as in any way injurious to agriculture or otherwise, but the brilliant little "chafer" *Pyronota festiva* F. has been known to work considerable havoc with the blossoms of fruit-trees, and cereal crops and pastures are sometimes greatly damaged by the larvae of one or two species of the Melolonthid genus *Odontria*. The huge white larvae of *Prionoplus reticularis*, called "huhu" by the Maoris, and greatly esteemed by them as an article of food, live in the timber of the Kauri and other Conifers, but the trees are probably attacked by the beetle only when they are in a state of incipient decay. Another of the larger Longicorns, *Aemona hirta* F., is sometimes destructive to orange and lemon trees in the North Island, as well as to the Puriri, or New Zealand teak (*Vitex littoralis*). This valuable timber tree is also subject to the attacks of the larva of the large Hepialid moth *Charagia virescens* Doubl., and sound logs are in consequence often difficult to obtain. Two weevils, *Mitrastethus bituberculatus* F. and the Cossonid *Xenocnema spinipes* Woll., are also at times somewhat injurious to Kauri and other Coniferous timber, and at Reefton, a mining town in the South Island hastily built of "Kahikatea" or so-called "white pine," I found that two or three of the native species of Cossonides, associated with incredible numbers of our familiar *Anobium domesticum*, had practically eaten up many of the houses, through the planking of which it was quite easy to thrust one's finger in places.

Like the Coleoptera, the Lepidoptera of New Zealand were for a long period regarded as being exceedingly poor in species, and generally of somewhat unattractive appearance. It cannot be denied that the butterflies and moths of the Islands include few forms of large size or bright colours, and that, as with the beetles, many groups of otherwise world-wide distribution are here strikingly deficient or entirely absent. But during the last half-century the number of known endemic Lepidoptera has been very greatly augmented by the researches of such diligent resident entomologists as Mr. C. M. Wakefield, Mr. R. W. Fereday, Prof. Hutton and Mr. G. V. Hudson, whose finely illustrated and most useful work "New Zealand Moths and Butterflies," published in 1898, marks an era in the study of the fauna of the Dominion. Even a greater debt is owing to Mr. E. Meyrick, who resided and collected actively in New Zealand for some years. Besides publishing the descriptions of a multitude of hitherto unknown species, chiefly in the "Transactions of the New Zealand Institute," he has in the same journal, between the years 1910 and 1917, revised and brought up to date our knowledge of nearly all the principal sections of the Order, as represented in the region. The extreme importance and interest of the

New Zealand Lepidoptera from an evolutionary standpoint, as well as of their geographical relations with the insect faunae of other regions in the Southern Hemisphere, are clearly shown in this series of masterly papers, my indebtedness to which in this Address I here gratefully acknowledge.

The number of species of Lepidoptera at present known from the New Zealand region reaches the respectable total of 1078, and their distribution among the principal sections of the Order is shown in the following Table.

TABLE OF NEW ZEALAND LEPIDOPTERA

Division or Family.	No. of		Endemic.	
	Genera.	Species.	Genera.	Species.
Rhopalocera	9	15	4	10
Sphingina	2	2	—	—
Arctiidae and Hypsidae	3	5	1	4
Noctuina	26	109	8	93
Geometrina	28	219	9	210
Pyralidina	33	216	12	204
Tortricina	19	115	7	109
Tineina	95	364	37	344
Psychidae	2	2	1	2
Hepialidae	2	18	1	18
Micropterygidae	3	13	2	13
Total	222	1078	82	1007

Even in comparison with the general paucity of butterflies in the extra-tropical regions of the Southern Hemisphere, the number of species found in New Zealand is exceptionally small for its area. Only fourteen species (or fifteen if we include the intrusive and perhaps not fully naturalised *Danaida plexippus* L.) may be regarded as permanent residents; and these belong to only four main divisions, the almost universally distributed *Papilioninae*, *Pierinae*, *Erycininae*, and *Hesperinae* being totally unrepresented. Three of the five Vanessids, *Precis villida* F., *Pyrameis itea* F., and the almost ubiquitous *Pyrameis cardui* L. (var. *kershawii* McCoy), are well-known Australian forms, and the irregularity of their occurrence in different years suggests the probability that in

New Zealand their numbers are at times reinforced by migration from that continent across the Tasman Sea, with the aid of the prevailing strong westerly winds of those latitudes. One of the *Lycaenidae*, *Zizera labradus* Godt. (*Lycaena phoebe* Murray), is widely distributed throughout Australia and the Pacific Islands. The remaining ten species form a little endemic group of exceptional interest. The most showy butterfly is the beautiful *Pyrameis gonerilla* F., which represents our "Red Admiral" in the Dominion, and greatly resembles it in appearance and familiar habits; its larva, too, feeds in a closely similar manner on the big shrubby nettle *Urtica ferox*, in little tents made of leaves spun together. It is generally common throughout New Zealand, from the North Cape to Stewart Island, and is represented in the Chatham Islands by the closely allied *P. ada* Alfken. Three pretty species of *Chrysophanus* are also widely distributed; *C. salustius* F. is the commonest of these, the more handsome *C. feredayi* Bates being somewhat more local, and the larvae of both species may be found feeding on the imported sorrel in the same way as that of our *C. phlaeas*. The little purple-flushed *C. boldenarum* White occurs, sometimes abundantly, in dry stony places and shingly river-beds, and the inconspicuous *Lycaena oxleyi* Feld. is usually met with in similar situations.

By far the most interesting butterflies in New Zealand are the four endemic species of *Satyridae*, each one being the sole representative of its genus. *Dodonidia helmsi* Fereday, a somewhat rare and very richly coloured insect, flies in February in sunny openings in the forests on both sides of Cook's Strait, usually at a considerable height above the ground, and its capture is thus by no means easy; the food-plant of its larva is the large sedge or "cutting-grass," *Gahnia setifolia*. The other three species are, so far as is known, entirely confined to the South Island. *Argyrophenga antipodum* Dbld. is the characteristic butterfly of the "tussock-lands," its range extending from near sea-level to upwards of 4000 feet, and where it occurs it is often very abundant. The underside of the wings of this butterfly, with its longitudinal silvery stripes on a ground-colour of soft ochreous-brown, is very conspicuous in the cabinet; but when it is at rest at the bottom of a "tussock," these markings harmonise most perfectly with the lights and shadows of the yellowish grass-stems, and in this environment the insect presents as complete and beautiful an example of protective resemblance as our own "Orange-tip" on its favourite white Umbelliferous flowers. *Percnodaimon* (*Erebia*) *pluto* Fereday is in appearance and structure, as well as in habits, wonderfully like some of the black Erebias of the European Alps, and is fairly widely distributed and sometimes common on shingly mountain slopes at elevations between 4000 and 6000 feet. As I have unfortunately no practical experience of this mountain butterfly, I cannot refrain from quoting the very interesting remarks of Mr. H. Hamilton on the habits of the insect as observed by him in its native surroundings.* "*Erebia pluto* can only be located when the sun is shining strongly and continuously. This beautiful black butterfly is then to be seen hovering over the shingle-slips, and apparently following well-defined air-tracks. It was noticed that the best way to capture them was to sit close to a place they had been seen to pass, and keep perfectly still. Presently one would come sailing along, and apparently not notice the collector. A very quick movement with the net was necessary to catch the insect, and if you missed the first stroke the chances were all on the butterfly escaping. On being disturbed they make rapid jerky upward movements, and soon get out of the danger-zone, flying away to some other slope. As soon as the sun is obscured by a cloud all the butterflies alight and remain motionless until the sun shines again. As sunshine is the exception rather than the rule on these mountain-tops, *Erebia*-hunting is very trying to the patience."

Erebiola butleri Fereday is also restricted to similar high altitudes, but is a much more local and less common insect than *P. pluto*. To quote Mr. H. Hamilton again: † "As a rule, the habits of the *E. butleri* are sluggish, and it does not make long flights; it frequents some particular tussock-clump and flutters about there. The position of the female is generally indicated by watching the movements of the males, and noticing where they hover for a longer time than usual. During the bright sunshine the male *butleri* is seldom ever seen at rest, and appears to fly backwards and forwards along well-defined routes within certain natural boundaries. This 'trade-route' habit is specially characteristic of *E. pluto* also."

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* Trans. N.Z. Inst., XLIII, p. 117.

† L.c., p. 122.

In addition to the endemic butterflies of New Zealand, several wanderers from other regions have occasionally been found within its limits. Writing as long ago as 1855, the Rev. Richard Taylor, in his very interesting work "Te Ika a Maui," mentions "a fine large butterfly, closely resembling the English Purple Emperor," as being found in the Middle (South) Island; and in the second edition of the book, published in 1870, is a tolerable coloured figure of the male of *Hypolimnas bolina* L. under the Cramerian name of *Diadema auge.* This butterfly has been taken not unfrequently in recent years, and the large size and fine colouring of the specimens, notably of the female figured by Mr. Hudson in "New Zealand Moths and Butterflies," would appear to point to North Australia as their place of origin. *Limnas chrysippus* L., *Catopsilia catilla* Cram., and an unidentified species of *Euploea* are exceedingly rare visitors, also in all probability from Australia. More difficult of explanation is the undoubted occurrence, at Wellington in 1881,* and at Orepuki, at the south extremity of the South Island in 1903,† of several specimens of our *Pyrameis atalanta,* whose nearest station, to which it has found its way from North America, is in the Hawaiian Islands, at least 4000 miles distant from New Zealand. Even more inexplicable is the reported capture of *Aglais urticae* at Wellington, at the same time as that of *P. atalanta,* by Mr. T. Kirk; and I understand that even our *Pieris rapae* has on one occasion been observed at this port, having almost certainly been brought thither by chance in one of its early stages.

The powerful flight and wandering propensities of the *Sphingidae* have carried certain species of the family to some of the most remote oceanic islands, but only two have been observed in New Zealand. These are *Herse convolvuli* L., which, although by no means generally common, appears to be fully established in the Islands; and a few examples of the almost equally widely-ranging *Hippotion celerio* L. have been met with in recent years. The great assemblage of moths included under the obsolete but in some respects convenient name of the *Bombycina* are all but unrepresented in the fauna, several important families, as the *Limacodidae*, the *Lasiocampidae*, and the *Saturnidae*, being entirely absent; the sole representative of the *Hypsidae* is *Deilemera annulata* Boisd., whose sharply contrasted black and white markings and diurnal flight render it one of the most conspicuous and familiar of the insects of New Zealand. The very few *Arctiidae* include the widely distributed *Utetheisa pulchella* L. which is a fairly frequent visitor and perhaps established in the North Island, and three species of *Metacrias*, an endemic genus probably most nearly related to the South European genus *Ocnogyna*. The males of these are handsome and very active little " tiger-moths," which fly in the sunshine at rather high elevations in the South Island, the females being practically apterous, and covered with a thick coat of yellowish hair-scales.

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* Trans. N.Z. Inst., XVI, p. 550.

† Id., XXXVI, p. 161.

We have yet another instance of unequal representation in the case of the Noctuid moths. In his " Revision of the New Zealand *Caradrinina*,"* Mr. Meyrick enumerates 97 species, and the researches of the resident Lepidopterists, not forgetting those of our Fellow Dr. G. B. Longstaff,† have added about a dozen more in recent years. Seven of the genera, and a very large percentage of the species, are entirely restricted to the New Zealand region, and the great majority of these are comprised in a single sub-family, the *Melanchrinae*, the genus *Melanchra* alone having no fewer than 37 species. The multitude of diversified forms until recently included under the comprehensive title of the *Quadrifinae* are here represented only by a very few stragglers, chiefly from Australia and the Pacific Islands; and within the limits of the region we also find *Heliothis armigera* Hubn., *Leucania* (*Aletia*) *unipuncta* Haw., *L. loreyi* Dup. (in the Kermadec

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* Trans. N.Z. Inst., XLIV, pp. 86–107.

† " Butterfly-hunting in Many Lands," pp. 449, 451, 474.

Islands), *Agrotis ypsilon* Rott., and even our little *Hypenodes costaestrigalis* Steph., all insects of nearly world-wide distribution. A good many of the endemic Noctuae are handsomely marked and attractive-looking moths, though few are of bright colour or more than moderate size; and they share with our species their susceptibility to the attractions of "sugar," which is resorted to by the resident Lepidopterists with as much success as at home.

The Geometrina form an outstanding feature in the Lepidopterous fauna of New Zealand. In number of species they are surpassed only by the Tineina, and in beauty of varied pattern and delicacy of colouring many are excelled nowhere else in the world. In the words of Mr. Meyrick,* "the group exhibits the same inequality of representation of families that has been noticed in the others; three-fourths of the whole number of species belong to the family *Hydriomenidae*, which is very adequately represented, while the *Selidosemidae* and *Monocteniadae* are very imperfectly exhibited, and the other families either wholly absent or indicated only by one or two casually introduced immigrants." The foreign element is here even less in evidence than in any other division of the Lepidoptera, and only some nine or ten of the 219 known species are found beyond the limits of the New Zealand region. A few species occur in open situations, but the greater number inhabit the forest, and in many cases their colour and markings exhibit a beautifully protective adaptation to their environment. The members of the genera *Notoreas*, *Dasyuris*, and *Arcteuthes*, are brightly coloured mountain insects which fly in the sunshine up to an elevation of 6000 feet, and are found mostly in the South Island, and the species of *Declana*, which include some of the most handsome of the indigenous moths, are distinguished by their robust build, strongly contrasted patterns, and in the commonest, *D. floccosa* Walk., for extreme variability in colour and markings.

The Pyralidina of New Zealand number 216 species, included in 33 genera, and as pointed out by Mr. Meyrick,† comprise

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* Revision of the New Zealand *Notodontina*, Trans. N.Z. Inst., XLIX, pp. 248–273.

† Revision of the New Zealand *Pyralidina*, Trans. N.Z. Inst., XLV, p. 50.

22 per cent. of the entire Lepidopterous fauna, a higher proportion than in any other region. This is mainly due to the enormous development of the *Crambidae*, *Crambus* alone containing 42 species; and especially to that of the genus *Scoparia*, of which no fewer than 92 endemic species are now known. It is only in the Hawaiian Islands, from whence about 60 species have been recorded, that we find this well-marked genus so largely in evidence. Many of the principal families are either absent, or barely represented by a very few stragglers or immigrants, but there are 16 endemic species of the *Pterophoridae*, and the widely distributed *Stenoptilia zophodactyla* Dup. has been found at Wellington. *Pyralis farinalis* L., *Plodia interpunctella* Hübn, and *Meliphora grisella* F. have also been introduced by commerce, and are now established in the Dominion. The Tortricina present a considerable variety of forms, nearly all endemic, but only one of these, *Cacoecia excessana* Walk. appears to be of economic importance, its larva sometimes attacking apricot and other fruit trees. The "Codlin Moth," *Carpocapsa pomonella* L., has been introduced into New Zealand, but fortunately has not there become so great a pest as in Australia and Tasmania.

In his "Revision of the New Zealand *Tineina*,"* Mr. Meyrick remarks that "the *Tineina* usually constitute more than one-third of the Lepidoptera of any given region, and this proportion is apparently maintained in New Zealand." As 364 out of the 1078 species now known from the region belong to this division of the Lepidoptera, this estimate of its representation is very nearly exact. Fully one-third of these, again, are included in a single family, the *Oecophoridae*, and only in Australia does this family bear as large a proportion to the entire Tineid fauna. On the other hand, the extensive family *Gelechiadae* is represented by only a few species, and the *Adelidae*, which Mr. Meyrick says (*l.c.* p. 206) are "an ancient family and present in all the other continental regions (for I consider New Zealand as a continent, or rather the remains of one)" are entirely absent. Our "Currant Clearwing," *Trochilium tipuliforme* Cl. has been introduced, and is now to be found throughout the Dominion; and the cosmopolitan

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* Trans. N.Z. Inst., XLVII, pp. 205–244.

Plutella cruciferarum Z. is here, as elsewhere, a serious pest to turnips and other crops of a similar kind.

The *Zygaenidae* are entirely absent, and there are only two species of the *Psychidae*. The large larva-cases of *Oeceticus omnivorus* Fereday, are conspicuous on many indigenous and imported trees throughout the Islands, but are said to be less common than in former years. The *Hepialidae* include several fine species, among them the largest Lepidopterous insect of New Zealand, *Charagia virescens* Dbld. This very handsome green moth, whose life-history is fully and admirably detailed by Mr. Hudson in his " New Zealand Moths and Butterflies," is by no means rare, especially in the North Island, though the perfect insect is not often seen, and most of the specimens obtained are bred from the pupa. The larva feeds in the solid wood of living trees, and from its large size is capable of doing a great deal of damage. For a long time this larva was supposed to be the host of the fungus *Cordyceps robertsii*, well known as a curiosity under the name of the " New Zealand Vegetable Caterpillar "; but the ground-feeding larvae of the allied genus *Porina* have recently been ascertained to be the true hosts of this singular parasite. The *Micropterygidae* of New Zealand are of exceptional interest as including, in the genera *Mnemearcha* and *Sabatinca*, the most ancient and primitive forms of Lepidoptera now existing. A single species of the last-named genus is known from Queensland, but with this exception, the three genera and thirteen species occurring in the Islands are strictly endemic.

In his valuable paper " On the Geographical Relations of the New Zealand Fauna," Prof. Hutton in 1872 wrote as follows *—" The Heteroptera are remarkable for their fragmentary character, and wide distribution. The 13 known species belong to 13 different genera and 9 families; and there are not more than 7 endemic species, three of which have not been properly examined, and may therefore be found to be identical with species inhabiting other countries. . . . In strong contrast to this stand the Homoptera, which include 19 species, of three (*sic*) genera only; *Cicada* having 12, and *Cixius* 7 species." But while a fair number of species have since been added, the Heteropterous fauna of New Zealand remains one of the poorest and most scanty of all, and this was certainly my own impression when I was collecting there. As revised by the late Mr. G. W. Kirkaldy in 1909,* the fauna now includes 48 Heteroptera and 39 Auchenorrhynchous Homoptera, and of these some 40 species are endemic. Almost without exception, the forms in the first division are of small size and obscure colouring, but the second includes an interesting series of nearly twenty endemic species of *Melampsalta* (*Cicadidae*) which are a conspicuous feature in the insect life of New Zealand. As in the Hawaiian Islands, there are no endemic *Aphididae*, though some introduced species are now common; but the *Coccidae*, which have been worked out in an admirable series of papers in the Transactions of the New Zealand Institute by the late Mr. W. H. Maskell, number upwards of 90 endemic species, besides a score or more introduced from other parts of the world.

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* Trans. N.Z. Inst., V, pp. 247–8.

Another very poorly represented Order is the Hymenoptera. As enumerated by Prof. T. D. A. Cockerell,† the *Anthophila* include only 18 species comprised in three genera, *Prosopis*, *Halictus*, and *Paracolletes*, the last-named being common to Australia and New Zealand. Dr. A. D. Forel ‡ records 19 species of ants, nearly all of which are endemic; and while the Fossores are not much better represented, and the true wasps are entirely absent, a fair number of the *Parasitica* have been described from the region. With the exception of a single species of *Xiphydria*, the Phytophagous Hymenoptera appear to be entirely wanting; and at present not more than 200 species of the Order in all are known from New Zealand, but further researches are sure to add considerably to this number.

We owe most of our knowledge of the New Zealand Diptera to Prof. Hutton and Mr. P. Marshall; and the Order is, next to the Coleoptera and the Lepidoptera, the most fully represented in the region. It includes some fine and curious endemic forms, the large and very rare Anthomyid, *Exsul singularis* Hutton, from Milford Sound in the South Island, being one of the most extraordinary flies known, its very broad and short wings giving it somewhat the aspect of a Stylopid on a large scale; and the larvae of the Mycetophilid *Bolitophila luminosa* Skuse, which live gregariously in a slimy web on damp banks in the "bush," well deserve the name of the "New Zealand Glow-worm." Although the Maoris assert that mosquitoes were unknown before the coming of the English, the endemic species are quite sufficiently bloodthirsty, though none of them appear to be bearers of malaria; and sand-flies (*Simulium*) are very troublesome in some places, especially in the rainy forests of the South Island.

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* Trans. N.Z. Inst., XLI, pp. 22–39.

† Proc. Acad. Nat. Sci. Philadelphia, LXVIII, p. 68.

‡ Trans. N.Z. Inst., XXXVII, pp. 353–355.

The few Trichoptera call for little remark, except that the larva of *Philaniscus plebeius* Mc.L. lives among seaweed on the coast between tide-marks, a habit almost or quite unique in the Order. In the genera *Stenosmylus* and *Drepanepteryx*, the Neuroptera-Planipennia includes several endemic forms of great beauty; and in the Odonata, of which ten species, comprised in five families and six genera, are restricted to the region, *Uropetala carovei* White, allied to the equally large Chilian *Phenes raptor*, is one of the finest dragon-flies in the world. Three peculiar species of *Termitidae* are found in New Zealand, but they do no appreciable damage. In the *Ephemeridae* are one or two exceedingly fine forms, of which the most noteworthy is *Oniscigaster wakefieldi* McL., with its extraordinary hind-body looking like that of some Crustacean. It is greatly to be regretted that this unique insect, as well as several others of its family, has been practically exterminated by the trout introduced in such numbers into the country during recent years.

Among the most conspicuous and remarkable of New Zealand insects are the apterous forest-crickets of the family *Stenopelmatidae*, known throughout the Islands by the Maori name of "Weta," and of which some thirty-five species have been recorded. The largest of these, the "Weta-punga," *Deinacrida heteracantha* White, whose body is nearly as bulky as that of a mouse, and whose stout spiny hind-legs are six inches in length, lives in holes in trees in the North Island. It is now extremely rare, having been, it is said, nearly exterminated by the introduced Norway rat, and commands a high price as a curiosity. The much commoner *Hemideina megacephala* Buller, which is also reported from Lord Howe Island, is not greatly inferior in size, and the huge head and mandibles of the male give it an equally formidable appearance; and the cave-dwelling species of *Pachyrhamma* are noteworthy on account of the inordinate length of their slender antennae. The single Mantid, *Orthoderes ministralis* F., is found also in Australia and Tasmania, and is perhaps a recent introduction, and the *Phasmidae*, of which there are some twelve species, include one or two forms of considerable size. Three or four *Blattidae* at most are indigenous; *Platyzosteria novae-zealandiae* Walk., a highly odoriferous cockroach which abounds under loose bark, is familiar throughout the Dominion under the name of the "Maori Bug." The large and stout *Anisolabis littorea* White is the only common species of the very few endemic *Forficulidae*; our common earwig has gained a footing in a few places, but is by no means the pest that it has become in Tasmania. Finally, the only *Siphonaptera* which are found in New Zealand appear to be the best-known and universal species of the Order, and two others attached to domestic animals. Dr. Dieffenbach, writing in 1843,* states that "the natives say that fleas were introduced by Europeans, and for that reason sometimes call them 'te pakeha nohinohi,' the little stranger," but as early as 1773 the Maori huts at Queen Charlotte's Sound were found by Capt. Cook's sailors to be "exceeding full of vermin and particularly fleas," † and these insects are no doubt coeval with the first human inhabitants of the Islands.

The insect fauna of the outlying islands of the New Zealand region, though as yet imperfectly known, presents many features of great interest. A few insects were obtained in 1909 by Mr. W. L. Wallace from the volcanic but forest-clad Kermadec Islands, some 500 miles north-east of the North Cape. The thirty-eight species of Coleoptera show marked affinity with those of New Zealand, thirteen being described as new by Major Broun. More than half of the 46 species of

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* Travels in New Zealand, II, Appendix, p. 291.

† G. Forster, Voyage round the World in H.M.S. "Resolution," I, p 201.

Lepidoptera, among which are three butterflies, *Melanitis leda* L., *Hypolimnas bolina* L., and *Pyrameis itea* F. are common species of wide distribution; ten are New Zealand forms, and eight are described by Mr. Meyrick as new. The notorious plague-flea, *Pulex cheopis*, has found its way to these remote islands, which swarm with rats; as well as our *Coccinella* 11-*punctata*, now abundantly naturalised throughout New Zealand.

The larger group of the Chatham Islands is about 450 miles east-south-east of Cook's Strait. They possess a luxuriant vegetation, with a good deal of forest, and the number of resident species of insects at present known will certainly be largely augmented by further research. Besides the butterfly *Pyrameis ada* Alfken, already mentioned, 106 species of Coleoptera have so far been recorded: 49 of these are endemic, the remainder being well-known New Zealand forms. They include 12 Longicorns, three *Anthribidae*, and eight *Cossoninae*, and the rare *Acalles fougeri* Hutton, is the largest and finest known member of this extensive genus.

The widely scattered island groups in the stormy ocean south and east of New Zealand, and the solitary Macquarie Island far to the south-west, have in recent years been visited by several naturalists; and the results of the scientific expedition despatched thither under the auspices of the Dominion Government in 1907 are embodied in the two fine volumes entitled "The Subantarctic Islands of New Zealand," published two years later. In this enterprise Entomology was most adequately represented in the person of our Fellow Mr. G. V. Hudson, whose researches, however, were confined to the Snares and the Auckland Islands. Six species of Coleoptera, including a fine new *Mecodema*, were found in the former little group, distant some sixty miles south-west from Stewart Island. From the Auckland Islands, so renowned among botanists for their beautiful and most peculiar Flora, some half-dozen species of beetles were obtained by the French Antarctic expedition under Capt. Dumont d'Urville in 1840; and this number was increased to thirty by Mr. Hudson. Nine additional species were found by Mr. Marriner, another member of the expedition, at Campbell Island, which lies about 180 miles south-east of the Aucklands, and possesses a somewhat similar flora, except that true forest growth is absent. The 46 species of Coleoptera now known from the Subantarctic Islands, the predominant groups of which are the *Carabidae* and the *Rhynchophora*, are referred to no fewer than 26 genera, eight of these being endemic. No butterfly was observed in these islands, and only one Noctuid moth, *Melanchra erebia* Huds., a species of rather striking appearance; some half-dozen *Geometrae*, and the same number of species of the dominant genus *Scoparia*; a remarkable new Pyralid genus and species, *Protyparcha scaphodes* Meyr., with one or two Micro-Lepidoptera; in all about twenty species, twelve of which are endemic, though obviously allied to New Zealand forms. Except the *Diptera*, of which one or two very remarkable apterous and semi-apterous species were met with, the other Orders are very scantily or not at all represented.

In Antipodes Island, 490 miles east-south-east of the South Cape of New Zealand, Prof. Hutton observed the conspicuous Hypsid moth *Deilemera annulata* Boisd.; besides this insect, only three Diptera and a bird-flea, *Goniopsylla kerguelensis* Tasch. have been recorded from this lonely speck of land. The even more desolate rocks a little to the northward known as the Bounty Islands, though they are without a trace of terrestrial vegetation, have produced a single Hydrophilid beetle, *Thomosis guanicola* Broun, a remarkable Stenopelmatid cricket *Ischyroplectron isolatum* Hutton, and two or three flies, all living in deposits of seaweed and guano at high-water mark. Macquarie Island, in latitude 54° 30′ S. and longitude 158° 50′ E., has a fair amount of vegetation, but its only recorded insects are two peculiar species of Diptera. The biologists of the recent Australian Antarctic Expedition found "numerous beetles under stones and moss" in this island; these apparently have not yet been described, but cannot fail to be of exceptional interest, and in all probability will prove to be related to the singular forms occurring in Kerguelen Island.

Two islands in a far more genial climate, included in the New Zealand zoological province, remain to be considered. Norfolk Island lies about half-way between New Caledonia and New Zealand, and its fauna and flora, although mainly

Australian in general character, exhibit unmistakable affinities with the latter. These are most pronounced in the case of the endemic birds, but among the Coleoptera are two species of *Xylotoles*, one of the most characteristic of the New Zealand Longicorn genera. Some thirty species of beetles have been recorded, but a much greater number must inhabit an island of such luxuriance and fertility. In Lord Howe Island, which is only 300 miles from the Australian coast, and more than twice as far from the nearest point of New Zealand, about 80 species of Coleoptera, included in no fewer than 68 genera, have been found; among these are two species of *Xylotoles* and two of *Somatidia*, the latter genus being otherwise restricted to New Zealand. Unfortunately the representatives of the other Orders in these very interesting islands appear to be almost unknown, except the butterflies, all of which are of Australian species with the exception of the fine *Papilio amphiaraus* Drury of Norfolk Island, which has its nearest ally in New Caledonia.

It will be evident from this general review that the outstanding feature of the insect fauna of New Zealand is its eminently precinctive and isolated character, which it exhibits in common with all the living productions of the region. The origin and affinities of these have been the subject for many years past of a large amount of speculation and discussion on the part of students of the geographical distribution of animal life; and the general constitution of the fauna may be stated in the words of Prof. F. W. Hutton, one of the most eminent of these *—"The fauna may be divided into a small aboriginal element, including species which have no near relatives elsewhere, and larger Malayan, Australian, and Antarctic elements, as well as several smaller ones. In many cases, however, it is hard to say in which group a species should be placed, for its relations are so widely scattered. Taking a broad view of the whole fauna, however, it may be said that the terrestrial portion is chiefly of Malayan origin, but with rather strong Palaearctic and Neotropical connections." The origin of the aboriginal element may date back as far as the beginning of the Tertiary period, and among the insects it probably includes

* Index Faunae Novae Zealandiae, Introduction, p. 5.

most of the *Colydiidae*, and such forms as *Brounia*, *Dendroblax*, *Camiaius* and others among the Coleoptera, *Oniscigaster* among the *Ephemeridae*, and the very primitive and archaic *Mnemearcha* and *Sabatinca* in the Micro-Lepidoptera, to mention only a few forms. Probably all these are relics of the fauna of a vanished continental land in the South Temperate Zone, of which the site is in part indicated by the relatively shallow soundings of the New Zealand Plateau. This may at some period of its existence have been connected with what is now South America, and by this "land-bridge" the Neotropical element, so plainly indicated in the Fauna and Flora of New Zealand, may have been transmitted. As pointed out by Mr. Meyrick, this affinity between the two faunae is very evident in the principal divisions of the Lepidoptera, and especially so in the *Geometrinae*; and I well remember how much I was impressed, when in New Zealand, with the strong general resemblance of many of the Geometrid moths to those I had made acquaintance with in Chile some twenty years previously. The nearest allies of the remarkable butterfly *Argyrophenga antipodum* are to be found among the Chilian *Satyridae*; and the very distinct Tipulid genus *Macromastix* is also represented in Chile as well as in Amboyna. This last, however, is evidently a form of very great antiquity and wide distribution in bygone ages, as Prof. Cockerell informs me that a species of this genus has been recently detected in a stratum of Oligocene age in the Isle of Wight.

In the three endemic species of *Chrysophanus*, and especially in *Percnodaimon pluto*, which is practically an *Erebia*, we find an unexpected and not easily explicable affinity with the Palaearctic fauna; and a slight relationship with that of the Ethiopian region is indicated in the Histerid genus *Sternaulax*, one of the two species of which is found in New Zealand, and the other in Madagascar. A much larger element appears to have been derived originally from what are now the Austro-Malayan and Melanesian regions by way of extensions northward of the former "Greater New Zealand" as indicated by shallower soundings in this direction. These "land-bridges," however, have long been severed by the subsidence of the greater part of this ancient land, which occurred before many of the more recently developed forms of life were in existence. The great gaps in the fauna of New Zealand are thus explained, and so great an amount of generic and specific evolution has taken place within its restricted limits since its final isolation, that the affinities already indicated alone remain to tell of the former connections of the Islands with other regions. The surrounding ocean, too, has in recent times proved to be an effectual barrier to the interchange of species. Even in the case of the nearest continental land, though such insects as the strong-winged *Pyrameis itea* and *Precis villida* and a few Coleoptera, chiefly Longicorns and small dung-beetles, have made their way from Australia to New Zealand across the stormy Tasman Sea, probably less than a dozen species of New Zealand beetles have been found in Australia. The *Chrysomelidae*, *Cetoniadae* and *Buprestidae*, which are there so fine and so well represented (one Buprestid genus, *Stigmodera*, alone including no fewer than 420 Australian species), are in the Islands entirely absent or represented only by a few small or obscure forms; and of the numerous and characteristic group of Australian weevils, the *Amycterinae*, only a single species has been found as yet in New Zealand.

Instances of the unique and precinctive character of this wonderful insect fauna may be multiplied as regards all the Orders; but sufficient has been said, I trust, to illustrate its surpassing interest and importance in the scheme of the life-history of our globe, and to emphasise the immediate and urgent necessity of completing our knowledge of the insect life of New Zealand, before many of its most interesting and instructive forms disappear for ever before the march of settlement and cultivation.

It only remains, in concluding this Address, to express my sincere thanks for the uniform kindness and consideration which have been extended to me by each and every Fellow of the Society during the period of my occupation of the Presidential Chair, as well as by the members of the successive Councils during the sixteen consecutive years in which I have had the honour to hold responsible office; and to congratulate the Society on the choice of the distinguished Zoologist whom you have elected as my successor.

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THE GEOGRAPHICAL DISTRIBUTION OF *DANAIDA PLEXIPPUS*, L. (*DANAIS ARCHIPPUS*, F.) WITH ESPECIAL REFERENCE TO ITS RECENT MIGRATIONS.

BY JAMES J. WALKER, M.A., R.N., F.L.S.

In a former volume of this Magazine (Ent. Mo. Mag., vol. XXII, pp. 217–224), shortly after the capture of a considerable number of specimens of *Danaida plexippus* in Britain had been recorded in our current Entomological periodicals, I was induced to publish some notes on this most interesting butterfly embodying my observations made during a voyage in H.M.S. "Kingfisher" in the Eastern and Central Pacific Ocean, and to speculate on the probable causes of the rapid spread of the species at that time taking place across the warmer parts of that ocean and the Atlantic. In the long interval that has elapsed since this paper was written, two more voyages to Australia and the Western Pacific, where the butterfly has now presumably established itself as a permanent member of the insect fauna of these regions, have enabled me to add very materially to my experiences on the subject of the life-history and the wanderings of *D. plexippus.* I therefore venture to submit to the readers of this Magazine a summary of the history of the recent wonderful extension of its geographical range, in the hope that a useful purpose will be served in bringing together the scattered records of many observers during the last half-century or more, and that these records will prove to be of interest to Entomologists in general.

Although up to a very recent date *Danaida plexippus*—to give the butterfly its most recent generic name as adopted by Dr. Karl Jordan and Prof. E. B. Poulton—has been regarded as an undoubted native of the New World, the evidence brought forward by the last-named distinguished Entomologist (Trans. Ent. Soc. Lond., 1908, pp. 449–452: Charles Darwin and the Origin of Species, pp. 152–164, 204 [1909]) appears, to myself at any rate, to be conclusive that so far from this being the case, it is really "a member of an Old World genus that has invaded the New." Its striking dissimilarity from all but a very few (obviously allied) forms of the multitude of American Danaine butterflies, and its equally striking resemblance in all its stages to the widely distributed and abundant Oriental *D. genutia*, Cram., had, it is true, not escaped notice previous to the appearance of Prof. Poulton's paper; but I cannot do better than to quote the learned Professor's own words in his masterly essay on "Mimicry in North American Butterflies" (Darwin and the Origin of Species, pp. 159–160). "The suggestion might perhaps be made that the New World forms of *Danaida* are the more ancestral, and that those of the Old World have been derived from them by migration westward. There is no reason for believing that the Danaidas of either geographical area possess a more primitive structure than those of the other; we are therefore driven to consult other lines of evidence. The following comparisons clearly indicate that *Danaida* is an Old World genus which has invaded America at no very remote period:—(1) the far larger number of the Old World forms and the greater degree of specialization by which some of them are distinguished; (2) the place of *Danaida* as one out of a number of nearly related genera making up the *Danaini*, a large and dominant Old World group, *per contra* its isolated position in the New World; (3) the highly developed and complex mimetic relationships of the Old World Danaidas." Again (l.c., p. 162), "There can be little doubt that *D. plexippus* invaded America by way of the north, probably following the line of the Aleutian Islands. In North America it possesses an astonishing distribution for a member of so tropical a group, ranging immensely further north than any Danaine in the world. Furthermore *D. genutia*, the probable representative of its Old World ancestor, extends far beyond the tropics into Western and Central China. A study of the distribution of the Asclepiad food-plants on the eastern coast of Asia might perhaps throw light on the problem." Further (l.c., p. 163), "It is probable that both the American Danaidas as they pressed southwards were 'held up' for a considerable time at the northern borders of the Neotropical Region, unable at first to penetrate that crowded area. Finally they burst their way through, and are now abundant throughout all the warmer parts of the region, the forms of *plexippus* extending further into the temperate south, just as in the Northern Hemisphere they range further north than those of *berenice*. We are made to realize the recent date of the invasion of South America when we remember that nowhere else in the world do Danaine butterflies of equal abundance range through a crowded area without producing any effect on any member of the Lepidopterous fauna, or without themselves being affected thereby,"

That the wandering instinct which in all probability carried the ancestor of *D. plexippus* in past ages from the Old World to the New still survives in full strength in its present-day descendant, is evident from its well-known migratory habits in North America, well summarized by the late Mr. J. W. Tutt in his admirable series of papers "Migration and Dispersal of Insects" (Ent. Record, 1900, pp. 182-6, 206–9). But as he goes on to say (l.c., p. 236), "Whatever interest may attach to what we may term the internal migrations of *Anosia archippus* within the Nearctic region, much greater interest is felt in its movements to distant parts of the world." It is the history of these movements that I now proceed to consider.

THE WESTWARD MIGRATION OF DANAIDA PLEXIPPUS.

I. NEW ZEALAND.

It is not a little singular that the first definite record of the occurrence of *D. plexippus* outside the American Continent was from so remote a locality as the North Island of New Zealand, at about the time when it first became a British colony.

In the "Transactions of the New Zealand Institute," vol. VI, pp. 183–6 (1874), Mr. R. W. Fereday published an interesting paper "Observations on the Occurrence of a Butterfly new to New Zealand," he having received a specimen of "a large handsome butterfly of the genus *Danais*," captured by Mr. F. H. Meinertzhagen at Waimarama, Hawke Bay, N.I., and identified as "*Danais erippus*" from a New South Wales specimen in the Canterbury Museum, Christchurch, sent by Mr. C. French—the insect having by that time established itself in Australia. Mr. Fereday, who in his paper adopts the Cramerian name *berenice* for the insect in question, thus proceeds (l.c., p. 183), "From Dr. Hector I have also received a specimen of this butterfly, taken last summer at Hokitika (west coast of South Island), where he saw it in great abundance; and since the capture of the first, Mr. Meinertzhagen has taken several more specimens at Waimarama. . . . . . He informs me that wherever he has seen the butterfly it has been flying high, but not swiftly, in sunny sheltered places among trees, and settling on them. He also saw it travelling fast over the country along the coast. The first he saw early in November, and the last he took the first week in April. All the Maories to whom he showed the butterfly said they knew it, and the old Maories say it is called 'Kākăhŭ,' and is in some years very plentiful. The caterpillar, they tell him, was very plentiful this year, and feeds on the pollen of the gourd which they grow in that part of the country (Hawke Bay). *They are unanimous in saying that the butterfly was there before any white man came*" (the italics are my own), "and the Rev. W. Colenso of Hawke Bay told Mr. Meinertzhagen that he saw it many years ago."

Mr. Meinertzhagen also obtained from his neighbour, Mr. Nairn, a coloured sketch made from memory, but clearly recognisable from the description given as that of the larva of *D. plexippus*; also three pupæ " short and stumpy, of a pale green colour and dotted with gold on the edge which covers the wings. The Maori to whom he showed them recognised them as the pupæ of the *Danais*. Unfortunately the rats got at them and destroyed them " These larvæ were found on " the *Gomphocarpus ovata*, one of the milk-producing plants, and a native of the Cape of Good Hope."

In the same periodical for 1877 (Tr. N. Z. I., vol. X, pp. 276–280) appears an interesting account by the Rev. W. Colenso of his breeding " *Danais berenice* " from larvæ found feeding on some " cotton-plants " grown from seed at Meeanee, Hawke Bay. This paper elicited a letter, under date February 17th, 1878, to Mr. Colenso from Mr. F. W. C. Sturm, which appears in full in Tr. N. Z. I., vol. XI, p. 305, and is of very great interest as fixing a fairly definite date when *D. plexippus* first came under the notice of a competent observer in New Zealand. Mr. Sturm thus writes—" In regard to the butterfly, *Danais berenice*, or a closely allied species (as per your paper on the same) the first time I saw it was at the Reinga, up the Wairoa River in Hawke Bay, in December, 1840, or January, 1841. In 1848 I captured a number at the Waiau, a tributary to the Wairoa; I cannot recollect how many, but it must have been eight or nine at least. . . . . . . Again, in 1861, I captured three on the Rangatikei River . . . . . . one of which I have still in my collection. Four years back I saw three or four in my garden here and two years ago there was a great number in my gardens, always keeping about the Lombardy poplars and *Houheria populnea*. . . . . . I certainly believe the butterfly to be indigenous and not introduced ; and my observations of it fully coincide with yours that while in certain years it is plentiful, in other years it is not to be seen."

Unless we accept as true the statement made by the Maoris to Mr. Meinertzhagen " that the butterfly was there before any white men came," which may point to a still earlier invasion of New Zealand by *D. plexippus*, Mr. Sturm's record given above is, as far as I can ascertain, the first indication of the great migrations of the insect.

In more recent years, although *D. plexippus* has been several times recorded in New Zealand, mainly from the neighbourhood of Cook's Straits (Hudson, New Zealand Moths and Butterflies, pp. 102–3) it seems except in one instance always to have occurred sparingly or singly, and would appear to be barely, if at all, holding its own in the Islands. This exception was at Wanganui (N. I.) in 1894, when

Mr. P. A. Marshall recorded it (Tr. N. Z. I., vol. XXVIII, p. 313) as "breeding in hundreds in Wanganui on plants of a species of *Gomphocarpus* in gardens, but not appearing the following summer." During the thirteen months, in 1901 and 1902, that I was continuously in New Zealand, I never had the good fortune to see a specimen on the wing, and my friend Mr. G. V. Hudson regarded it as distinctly a rarity in the Islands. *Gomphocarpus fruticosus*, R. Br. (*Asclepiadeæ*), the ordinary food of the larva at Sydney, is sometimes grown in New Zealand gardens under the name of the "cotton-plant," from the large seed-capsules full of white cottony down enveloping the minute seeds; and the West Indian *Asclepias nivea*, L., is recorded as "an escape from gardens near Auckland" (Cheeseman, Tr. N. Z. I., vol. XV, p. 287), but neither of these plants appear to have become naturalized to anything like the same extent as is the case with the first-named in Australia at the present time.

II. The Central and North Pacific Islands.

My own observations on the extension of the range of *Danaida plexippus* to the Marquesas, Society, Cook, Hervey, and other island groups in mid-Pacific, as well as those of Mr. G. F. Mathew in the islands further to the west in that ocean, which appeared in my former paper in this Magazine (l.c., pp. 219, 220, 224), have been embodied by Dr. S. H. Scudder in the admirable history of the butterfly in his monumental work, "The Butterflies of the Eastern United States and Canada." (Cambridge, Mass., 1889). The section entitled "Commercial Extension in Recent Years" (vol. I, p. 730 *et seq.*), deals with the question of its range over the Pacific Islands in so thorough and interesting a manner, that I make no apology for quoting it almost in full, though, as will be seen later on, I am by no means in complete agreement with some of his suggestions relative to the "means of dispersal."

"Among the most interesting points in the distribution of this butterfly is the fact that within 30 years or a little more it has begun to invade so many regions of the world as to make one think at first blush that it may some day vie with Vanessa cardui in cosmopolitan character. The facts concerning its exotic distribution, so far as I have been able to gather them, are as follows: It first reached the Hawaiian Islands, fully two thousand miles from America, some time not far from 1845 to 1850. At any rate we have the direct statement of Dr. Luther H. Gulick who was born upon the islands, that in 1852, after eleven years absence, he returned to the islands, and his brother drew his attention to the fact that Asclepias had been introduced during his absence, and had already become a troublesome weed; that his brother had noticed that where the milk weed appeared, there also the Anosia made its advent, a butterfly unknown until after the milk weed had been introduced. We next find it in 1857 as far away as the Island of Ponape (Ascension), one of the Caroline Islands in Micronesia, a distance of another two thousand miles or so from the Hawaiian Islands. This fact we also owe to Dr. Gulick's personal testimony. He was for some time a resident of Ponape, and the butterfly was first seen by him in the year mentioned, not long after he had discovered several young milk weeds, which had sprung up in earth in which various other plants had been brought from the Hawaiian Islands in a Wardian case. The plants were brought in a missionary vessel which sailed from Honolulu, and on its way to Ponape touched only at Apaiang of the Gilbert Islands and Ebon of the Marshall group, both low coral atolls, and at Kusaie, which is of basaltic formation and richly clothed with verdure, but where the butterfly did not then occur. It is evidently impossible that in a voyage consisting in the whole of fifty-four days, the insect in any stage or stages could have been transported in the Wardian case itself, for it easily undergoes all its transformations in warm regions in a month or five weeks at most. If the butterflies were introduced at that time, as there is every reason to believe from Dr. Gulick's accounts, there seems no other supposition possible than that an impregnated female flew into the hold of the vessel while lading at Honolulu, and was carried perforce to Ponape, or perhaps a pair of butterflies. It would certainly be absurd to suppose that a gravid female could have flown over the two or three thousand miles of ocean, and in addition have appeared in Ascension Island almost simultaneously with a few plants of Asclepias. As the butterflies pass the entire winter in hibernation, and then lay eggs in the spring, there is nothing in any way surprising in Dr. Gulick's statements, unless it be impossible for an impregnated female to live in enforced hibernation a couple of months without laying, when it would be necessary to suppose a pair to have been transported, which would of course be more extraordinary.

"Granting our explanation to be just, it is highly probable that it was from this single ancestor, or pair, that the swarms, which have already now spread over the entire South Seas, in many of which it is the commonest butterfly known, have sprung. Our knowledge of the period and extent of this later distribution we owe largely to Professor Semper,* who states that the butterfly was first seen in 1863 by Captain Rachan, one of numerous collectors of the Museum Godeffroy on the islands of the Tonga or Friendly group, again nearly 2,000 miles from Ponape. The first specimen actually obtained was secured in 1866 on Niuafau, one of the islands of this group, and in the same year larvæ were discovered on Asclepias curassavica, a plant now spread quite as far as the Anosia. We now begin to be able to record in part the rapidity of its spread; for it was first seen in Tutuilla, one of the islands of the neighbouring Samoan group, in 1867, but upon Upolu and Savaii, islands of the same Samoan group, distant at the nearest some fifty miles, not until 1869. Yet in Upolu it became one of the commonest butterflies in 1870. It was not until 1868 that it was discovered at Tongabalu (*sic*), one of the southern of the Tonga Islands, but in the same year it was seen in the open sea five hundred nautical miles to the south-east. In 1869 it had appeared at Roratonga, one of the Hervey Islands, five hundred miles or more away. In 1870 to 1872 it was found on Huahine and Tahiti, of the Society Islands, again five hundred miles or more distant. So far the account of Professor Semper. But Mr. James J. Walker, who sailed in the South Seas in 1883 and found Anosia nearly everywhere one of the commonest butterflies, states that he was informed at the Marquesas Islands, which lie to the north-east of the Society Islands, again at a distance of some five hundred miles, by a Roman Catholic missionary residing there forty years, that he distinctly remembered seeing the first specimen there about 1860; it should be noted that the Marquesas Islands are nearly as distant in a south-easterly direction from the Hawaiian Islands as the Carolines are to the south-west. Mr. Walker also found the butterfly on the Hervey and Society Islands, and at Oparo, one of the Andaman (*sic !*) group, in 28° south latitude, though it had not then reached Pitcairn Island, which lies much farther east and somewhat farther north. These statistics indicate its movements from the Caroline Islands in an easterly and south-easterly direction, but it has also left its mark by the way in a southward extension from this route of travel. . . . . . It reached Lord Howe's Islands in 1870, Clarence River on the opposite coast of Australia in 1871, Melbourne in 1872, and has now extended to Celebes, and, according to Kirby, to Java.

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* G. Semper on the appearance of *Danais archippus* in the South Sea Islands, Australia and Celebes; Journ. Mus. Godeffroy, II, pp. 117-119 (1873).

"It thus appears that it now possesses a territory in the Pacific Ocean of at least 110° of longitude and 65° of latitude. But this is by no means all. It has moved also in some strange way in the opposite direction from the American Continent."

In all these widely separated island-groups *Danaida plexippus* appears to have become one of the commonest butterflies in a very few years after its arrival, and the following passage from that delightful narrative of Pacific voyaging, "South Sea Bubbles," shows that not only was this the case in one at least of these groups, but that its American origin was there a matter of common knowledge. Writing of Samoa in 1870, one of the authors says:—"Coming down from our ravine, we pass through a wilderness of imported plants and shrubs, flourishing in wild luxuriancy. That red and brown flower, which makes such pretty wreaths for the girls' heads, and the down from whose pods is so dangerous to the eyes, is an importation, Heaven knows how, from America; and not only is it an importation, but it has imported its own butterfly with it, that splendid red and brown fellow who looks as if he had got half his colour from his native flower." More than twenty years after this date, Mrs. Jane Fraser (Ent. Mo. Mag., vol. XXX, p. 149) notes *D. plexippus* as "one of the first butterflies to be noticed in the Navigator (Samoa) Islands" and in Upolu it was very much at home, but was decidedly more numerous at a few hundred feet above the sea.

I am not aware of any very recent records from the Central Pacific, but I think there can be no reasonable doubt that both the butterfly and its most usual food-plant, are firmly and permanently established in the larger groups of islands. But as regards Micronesia, which consists with very few exceptions of coral atolls of no great size, and elevated only a few feet above the ocean level, it would appear that there *D. plexippus* exists on a very precarious tenure, and perhaps not at all as a permanent resident; though, as already stated, Ponape in the Carolines has been suggested by Dr. Scudder as one of the chief centres of distribution in the Pacific. Mr. Mathew (Ent. Mo. Mag., vol. XXII, p. 220) did not meet with it in his cruise among the Gilbert, Ellice, Marshall, and Caroline Islands, though he saw *Asclepias* in the last-named group; neither is it included in the list of butterflies collected by the Rev. S. J. Whitmee in the Ellice Islands (A. G. Butler, P.Z.S., 1878, pp. 296–7), nor in those found by Mr. C. M. Woodford in Nukufetau, Ellice Is., Tarawa and Tapetewea, Gilbert Is. (A. G. Butler, Ann. Mag. Nat. Hist. [5], XV, pp. 296–7). Again, in the small list of insects collected by Mr. C. Hedley during the coral-boring expedition in 1896 to Funafuti in the Ellice Group (Rainbow, Memoirs Austr. Museum, III, part ii, p. 95), there is no mention of the occurrence of *D. plexippus*, nor is *Asclepias curassavica* included among the few plants noticed by him or by subsequent visitors as growing on that atoll. It is quite possible that the conditions of these small islands do not favour the growth of the plant.

III. The Western Pacific, Australia, the Malay Archipelago, &c.

The very interesting records of *Danaida plexippus* in the Western Pacific Islands, by my friend Paymaster-in-Chief G. F. Mathew, R.N., nearly thirty years ago, have been included in my previous paper (Ent. Mo. Mag., vol. XXII, pp. 220, 221), and have been supplemented by my own observations made in 1900 in New Caledonia, the New Hebrides, and the Loyalty Islands (*l. c.*, vol. XXXVIII, p. 192, *et seq.*). I have, however, been unable to collect any information as to the date at which it first made its appearance in any of these island groups; but it probably reached this region very shortly after its arrival in the Central Pacific.

In the "Field" of April 16th, 1881 (p. 539), Mr. E. L. Layard gives the following very interesting notes on the butterfly and its food-plant as observed by him at Teremta, a French military post on the west side of New Caledonia, some sixty miles north of Nouméa— "A burst of sunshine and we are out on a sandy flat, also evidently subject to frequent overflow of the river . . . . but now covered with a luxuriant growth of the pest-weed of that country, the "gensdarmes plant" as it is called, second only to the *Lantana* in its powers of expansion and destructiveness. . . . . Millions of huge red-brown butterflies sported among the flowers of this useless plant, their larvæ devouring the leaves in spite of the acrid milky sap they contain. It is strange that both plant and insect are introductions, and not natives of the colony. The former, an Asclepiad, is said to have been brought from Tahiti by a gendarme who had stuffed his mattress with the silky cotton of the pods. This he emptied out in his barracks near Nouméa, and the few chance seeds clinging to the cotton, finding a suitable soil, established themselves, and have thence spread all over the land. The butterfly (*Danais*) is an American insect that appeared suddenly in Australia. It was apparently introduced here in a case of plants by Père Montrouzier, the celebrated

French naturalist, from thence, and has followed the plant in its migrations."

It is just possible that in this instance the butterfly was introduced into New Caledonia by the worthy Father with a view to its utility in keeping down a noxious weed; indeed, the ravages of the larva, as suggested by Mr. Layard, would appear a few years later to have so far destroyed the *Asclepias* as to cause a noteworthy reduction in the numbers of the butterfly through want of food (*cf.* Ent. Mo. Mag., vol. XXII, p. 220). Certainly when I visited New Caledonia and the Loyalty Islands in 1900 (l.c., vol. XXXVIII, pp. 192, 201), the *Danaida* and the *Asclepias*, though both plentiful enough, could not have been called superabundant. However, I prefer to think that the insect found its way to New Caledonia, as to the other localities in the Pacific Ocean, without definite human aid.

As early as 1870 we find the *Danaida* recorded in considerable numbers at Brisbane, Queensland, by Mr. W. H. Miskin (Ent. Mo. Mag., vol. VIII, p. 17). At about the same time the butterfly was found at Rockingham Bay, on the coast, 1500 miles to the north of Brisbane. Prof. F. McCoy, Director of the National Museum of Victoria, gives a very interesting account of the sudden appearance of *D. plexippus* at Melbourne (Ann. and Mag. Nat. Hist. (4), XI, pp. 440–1) (1893), which I quote at some length :—" This fine butterfly was sent to me about December, 1870, from Lord Howe's Island, on the north-east coast of Australia, by a collector for the Museum, who was wrecked there ; but as I had never seen it in any of the North-Australian, or Queensland, or New-South-Wales collections, and knew it to be an inhabitant of the Southern States of America, I suspected that the specimen might have been obtained from some collector on board some American ship in those seas. A few months after, a specimen was sent to me by a collector established on the Clarence River, in New South Wales, as something he had not seen before, and another friend, fond of insects, travelling in the far north of the continent, also sent me an example as something strange. As there were no exact accounts of the actual capture of these specimens, I fancied they all might have come from some one American source, and paid little attention to the matter. On the last Sunday in April last (1872), or about a year and five months after, I was walking in my garden at Brighton, a place on the sea-shore about eight miles south of Melbourne, and was astonished to see that a larger butterfly with a more bat-like flight than any inhabitant of the colony, which attracted my attention among the flower-buds, was the *Danais archippus*; and presently the two sexes were seen. Being Sunday, they escaped; but next morning, going through the grounds of the University on the north side of Melbourne. . . . I observed two more before me, and on going to my room found my collector in a great state of excitement at having caught one in my botanic garden in the University grounds, and having the previous day seen one five miles south of Brighton. So that the insect had made its appearance for the first time in the colony simultaneously at places fourteen miles apart, and with no community of character or vegetation. On the three following Sundays I saw two or three specimens in fine condition, which could not, therefore, have been those seen at first; and last week (end of March, 1873), I saw some in the street leading to the University, and on the same day the collector came across them . . . . at the opposite side of the city . . . . This sudden American invasion of the whole continent seems worth recording."

It is evident that New South Wales was reached by *D. plexippus* very soon after its first arrival in Australia. Mr. G. A. Waterhouse states (Proc. Linn. Soc. N. S. Wales, 1897, p. 286) that "since 1870, it has been a very familiar insect about Sydney." An indication of an even earlier arrival is, however, given by Mr. A. S. Olliff on p. 10 of his little work on "Australian Butterflies" (Sydney, 1889). He says: "It is generally thought that 1870 was the first year of its appearance here (at Sydney), but Dr. Ramsay of the Australian Museum informs me that he is positive that he saw the species at Ashfield, near Sydney, as early as the year 1856. Observers are so scattered, that the exact date of the insect's arrival can only be a matter of conjecture. It is evident, however, that the species did not obtain a firm foot-hold until 1870 or thereabouts." It was the very first butterfly that I saw on the wing at Sydney, in February, 1900, and on all my visits to that port I found it in more or less abundance. Here I may record an unpremeditated experiment which clearly demonstrates the extreme unpalatability of the insect in the larva state. One day in May, 1903, while my friend Mr. H. J. Carter and I were lunching in the garden of the hotel at Narrabean, a few miles north of Sydney Harbour, a small pet monkey picked my pocket and made off with a pill-box containing two full-fed larvæ of *D. plexippus*. She at once proceeded to devour the tempting-looking caterpillars, and it will be long before I forget the expression of supreme disgust on the face of the little creature when she realised the flavour of her supposed prize, nor the ludicrous haste with which she rejected the nauseous mouthful, even rubbing her tongue vigorously on the grass for some time to get rid of the taste.

A large portion of the Australian Continent is apparently as yet unoccupied by *D. plexippus*, as during the voyages of H.M.S. "Penguin" to the North-West Coast in 1890 and 1891 I did not observe it in any of the numerous localities visited by the ship between Port Darwin and Shark's Bay, nor had it at that period reached the more settled districts of Western Australia. Directly we entered the Malay Archipelago, however, the butterfly put in an appearance, and I have recorded it from Damma, Amboyna, and Ternate (Ent. Mo. Mag., vol. XXIX, pp. 25, 27, 30). At Damma I had another convincing demonstration of the insect's inedibility, this time of the imago. I had lain down to rest under a shady tree one very hot afternoon, and on waking after a short doze, was horrified to find that a swarm of black ants had found their way into my cork helmet, pinned full of my day's catch of butterflies, and that nearly all its contents were reduced to rags. The sole exceptions to the general destruction were one or two Euplœas and the single *Danaida plexippus*, a large ♀, that I had seen on the island. These the ants had left absolutely untouched.

In the Philippine Islands, as well as at Hong Kong, I failed to meet with *D. plexippus*, though in the latter island I saw plenty of *Asclepias curassavica*, which is there a favourite food-plant of the larva of *D. chrysippus*. On the evidence of a single specimen in the Oxford University Museum labelled "Hong Kong 1896-7 ex Swinhoe," it would seem to have found its way there since my visit. Among further records from the Eastern Archipelago, I may notice that Dr. W. J. Holland, in the "Twenty-fourth Annual Report of the Entomological Society of Ontario" writing in 1893 "On the Occurrence of *Danais plexippus* in consignments of Eastern *Lepidoptera*," remarks: "One of the sendings was from Borneo, the other from Java. We shall soon hear of its domestication on the mainland of Asia, and it will probably spread all over China and Japan." Yet more interesting, as being in all probability the farthest record of the insect in a westerly direction from America, is that by Mr. L. de Nicéville and Hofrath Dr. L. Martin in "A List of the Butterflies of Sumatra" (Journal, Royal Asiatic Soc., Bengal, vol. LXIV, pp. 366-7)—"Mr. W. F. Kirby has already recorded it from Java. I now for the first time, I believe, record it from North Borneo, the late Mr. W. Davison having sent me a male specimen from that island . . . . Furthermore, the late Mr. E. F. T. Atkinson in 1889 presented a female specimen of this species to the Indian Museum, Calcutta, which was captured on April 19th, 1889, by Mr. C. White, the chief officer of the P. and O. S.S. "Ravenna," in the Strait of Malacca (which is, at the point where the butterfly was caught, only a few miles broad). It is therefore not at all improbable that the butterfly flew from either the adjacent island of Sumatra or the Asiatic mainland." In the same paragraph the authors remark that —"In Part II of a new edition of Morris's History of British Butterflies, p. 72, it is stated to have been found in the Andaman Islands." This record, if correct, would carry the butterfly still farther on its westward course; but it is quite possible that in this case the common Oriental *D. genutia* may have been mistaken for *D. plexippus*; or it may even be that the unaccountable erratum of Dr. Scudder (l.c., p. 732) in referring Oparo in the Central South Pacific to the "Andaman group," has given rise to the statement.

In January, 1904, when on my voyage home from Australia in H.M.S. "Diadem," the ship called at the Cocos-Keeling Islands (lat. 12° S., long. 97° E.). During the short time that I was on shore there, one of the two species of butterflies seen by me on the wing was *Danaida chrysippus*, a certain indication of the presence of an *Asclepias*, though I did not actually see the plant growing. In his list of Keeling Atoll plants made in 1879 (A Naturalist's Wanderings in the Eastern Archipelago, p. 43), Mr. H. O. Forbes includes *Asclepias curassavica*, and states (*l.c.*, p. 31) that its flowers are "frequented by several moderately large diurnal species of *Lepidoptera*." The food-plant of *plexippus* is therefore ready for the butterfly, should it any time be blown to that remote atoll by one of the cyclones which are known to carry many other insects thither (*cf.* Forbes, *l.c.*, pp. 30, 31). A long way further to the west and north, when passing through the Suez Canal in June, 1893, I saw *Asclepias curassavica* growing luxuriantly at Ismailia, and attended by numbers of *D. chrysippus.*

THE EASTWARD MIGRATION OF DANAIDA PLEXIPPUS.

I. BERMUDA, THE AZORES, AND THE CANARY ISLANDS.

Turning now to the wanderings of *Danaida plexippus* eastward from the American Continent, we are not surprised to find that at the Bermudas, the first island group encountered in this direction, the butterfly has been long established as a resident, and together with its food-plant has found there a congenial home. It would indeed be remarkable if this strong-flying insect had not many times succeeded in making the passage thither, with the aid of the heavy autumnal gales which sweep across the 650 miles of ocean that separate the coast of Carolina from the Bermudas, and carry to the Islands so many species of North American birds of limited powers of flight, and even swarms of such a small and feeble butterfly as *Terias lisa*, Boisd. (*cf.* Wallace, Island Life, ed. 1892, p. 269; J. Matthew Jones, The Naturalist in Bermuda, p. 120). The notice of our butterfly as observed by Mr. Jones in Bermuda, is as follows (*l.c.* pp. 118–9) :—

"Of the few species of Diurnal Lepidoptera frequenting the Islands, the Archippus butterfly (*Danais Archippus*) ranks first for size and beauty. This fine species, which is so frequently seen in the southern states of America, is also common in the Bermudas, and generally to be found where a patch of ipecacuanha is in bloom. Mr. Hurdis' note-book has the following :—'Dec. 18. The beautiful caterpillar of *D. Archippus* is still common' (here follows a brief description of the larva and pupa). 'The favourite food of the caterpillar is the curascoa swallow-wort or bastard ipecacuanha (*Asclepias curassavica*) which grows wild in pastures, gardens, and roadsides, and blossoms during every month of the year. The perfect insect is abundant throughout the year.'" *D. berenice*, Cram., a well-known species from the warmer parts of America, is recorded (*l.c.*, p. 119) as "of rare occurrence in the Bermudas."

We owe the first record of *Danaida plexippus* from the Azores to Mr. F. Du Cane Godman (The Natural History of the Azores or Western Islands, pp. 101–2). Under "*Danais archippus*, F.," he writes—"I met with only two specimens of this insect, neither of which did I catch myself. One was taken in Flores in 1864, the other kindly given me by Mr. J. Dabney of Fayal, where it had been caught the previous summer (1864). Both specimens are females . . . . I do not regard the species as established in the Azores, though the fact of its having been obtained from two islands so widely separated is a curious coincidence, and not easily accounted for. I met with no one who knew the insect or had ever seen it before. I may also add that there is regular communication between North America and the Azores."

A subsequent capture of the butterfly in these Islands is noted by Dr. W. J. Holland (Twenty-fourth Annual Report of the Entomological Society of Ontario, 1893—"The insects taken by the United

States Eclipse expedition of 1889, at the Azores, numbered among them two specimens of this butterfly. There were only about a dozen specimens of insects taken at the Azores by the industrious naturalists of the party, and I judge that it must be common there. Why we have not heard of its domiciliation on the African continent is a mystery to me. It will no doubt get there before long." It is not, however, enumerated in the list of species of *Lepidoptera* met with in the Azores by Dr. Ernst Hartert and Mr. W. R. Ogilvie-Grant in March and April, 1903 (Warren, Novitates Zoologicæ, vol. XIII, pp. 439–447), and is probably little more than a casual wanderer to these Islands; neither is *Asclepias curassavica* included in Mr. H. C. Watson's catalogue of the Azorean plants in Mr. Godman's book, though he notes (pp. 194–5) *A.* (*Gomphocarpus*) *fruticosa*, L., from Fayal, but as " only a casual escape from gardens."

At the present time the Canary Islands are the head-quarters of the butterfly in the Eastern Atlantic region, though I have not been able to ascertain the exact time at which it first reached these islands, or at any rate was first observed there. I had no record of its occurrence in the Canaries in my former paper (1886), but my friend Prof. Poulton writes (Bedrock, April, 1914, p. 42, footnote)—"I saw it myself in Grand Canary in 1888," and in February, 1889, I was shown at Gibraltar several specimens that had been taken in Teneriffe only a short time previously. It would appear, as well as its food-plant, to have increased and multiplied rapidly since that time, for in 1894 we find Mrs. A. E. Holt-White (The Butterflies and Moths of Teneriffe, pp. 44–46) writing as follows—"The larva . . . . lives and feeds gregariously on the 'Arbol de Seda' (silk-tree, *Asclepias curassavica*), a plant bearing a very bright red and gold flower . . . . A brood seems to emerge about every three months in most years from February to September. The butterfly frequents flower-gardens and fields near the coast, not often being found more than seven or eight hundred feet above the sea." Subsequent records from the Canaries agree as to its now being one of the common butterflies of the Islands, and Mr. A. E. Elliott (Ent. Mo. Mag., vol. XXXVIII, p. 131) notes it as being "fairly common and widely distributed" in the winter months of 1901–2.

I can find no record of the occurrence of *Danaida plexippus* in Madeira, though as long ago as 1885 I was shown in an English greenhouse a vigorous plant of *Asclepias curassavica* which had been brought from that island.

II. THE BRITISH ISLANDS.

The recorded occurrences of *Danaida plexippus* in our islands, which I have been able to collect from the various entomological magazines, &c., may be conveniently presented in the following table:—

DATE.	LOCALITY.	AUTHORITY.	WHERE RECORDED.
1876, Sept. 6	Neath, S. Wales	J. T. D. Llewellyn	Ent. Mo. Mag., IX, pp. 256–7.
,, Sept. (2nd week)	Keymer, Sussex	F. Bond	Entom., X, p. 73.
,, Oct 17th	Hayward's Heath, Sussex	Rev. T. E. Crallan	Entom. IX, pp. 265–7.
1876–7	Poole, Dorset	Rev. A. E. Eaton	Ent. Mo. Mag., XXII, p. 161.
1881, Sept. 21st	Snodland, Kent	J. Jenner Weir	Entom., XIX, p. 12.
1884, Sept. 12th	Ventnor, I. W.	D. Westropp	Ent. Mo. Mag., XXI, p. 202.
1885, August	Exmouth, Devon	Rev. J. Hellins	Ent. Mo. Mag. XXII, p. 211.
,, Sept. (early)	Ventnor, I. W.	J. Jenner Weir	Entom., XVIII, p. 306.
,, Sept 17–24th	Lizard, Cornwall (3 specimens taken, another seen)	A. H. Jenkin	Entom., XVIII, pp. 291–2.
,, Sept. 21st	Land's End, Cornwall	R. J. Anderson	Entom. XVIII, p. 291.
,, Sept. 26th	Parkstone-on-Sea, Dorset	T. G. Cuthell	Ent. Mo. Mag., XXII, p. 134.
,, Sept. (end)	Castlemartin, Pembrokeshire	Rev. Clennell Wilkinson	Entom. XIX, p. 298.
,, Sept. (end)	Downderry, Cornwall	F. F. Freeman	Proc. Ent. Soc. Lond., Oct. 7th, 1885.
1886, Aug. 19th	Swanage, Dorset	J. E. Mowlem	Entom, XIX, p. 247.
,, Sept. 30th	Bournemouth, Hants	W. McRae	Entom. XIX, p. 277.
,, Oct. 2nd	Guernsey, Channel Is.	W. A. Luff	Entom. XIX, 278.
,, Sept. or Oct.	Lizard, Cornwall (seen)	A. H. Jenkin	Entom. XIX, 276.
(No date)	Cornwall	Mr. Saundry	Entom. XXIX, p. 59 (Tugwell's sale).
(No date)	Shanklin, I. W.	J. A. Billings	Entom., XX, p. 39.
1887, Sept. 14th	Worthing, Sussex (one taken, another seen)	F. H. Stewart	Entom. XXI, p. 321.
1890, Oct. 2nd	Eastbourne, Sussex (seen)	A. H. Clarke	Ent. Mo. Mag., XXVI, p. 327.
1895 (*circâ*)	Shanklin, I. W.	Hubert F. Poole	Guide Nat. Hist., I. of Wight, p. 398.
1896, May 28th	Lymington, Hants	E. G. B. Meade-Waldo	Field, June 6, 1896.
,, Sept.	Lizard, Cornwall (seen)	A. H. Jenkin	Entom., XXVI, p. 327.
1908, Sept. 13th	Culver Cliffs, I. W.	Hubert E. Poole	Guide, Nat. Hist., I. of Wight, p. 398.

It will be seen at once that of the twenty-nine specimens enumerated above as having been captured or seen within the limits of the British (and Channel) Islands, every one has occurred in a maritime county, and with only two or three exceptions, on the coast itself. Cornwall heads the list with nine records, the Isle of Wight and Sussex have five each, Dorset three, Hants and South Wales two, and Devon, Kent, and Guernsey one apiece. The absence of any records from Ireland is noteworthy, especially when the relatively large number of captures in the western parts of England is taken into account, but this may well be due to the lack of observers on the Irish coast.

III. THE CONTINENT OF EUROPE.

The number of specimens of *Danaida plexippus* that have reached the shores of Continental Europe is unaccountably small in comparison with the fairly numerous occurrences of the butterfly in Britain. I am unable to add any further records to those of its capture by M. Grassal, in La Vendée, Western France, in September, 1897 (Baret, Pet. Nouv. Entom., II, pp. 253–4); my own note in this Magazine (vol. XXIII, p. 162), on the specimen taken by Lieut. C. H. Cochran, at Gibraltar, on October 24th, 1886, almost on the day of my arrival there from England; and the record by the late Mr. H. Goss (Entom., vol. XX, p. 106) of the capture by Mr. Geo. D. Tait of a ♀ specimen, on September 29th, 1886, in his garden at Oporto.

THE RANGE OF DANAIDA PLEXIPPUS IN THE NEW WORLD.

Before proceeding to enquire into the agencies that have been the cause of the spread of our butterfly to the remote shores it has now reached, it is desirable to indicate the limits of its distribution throughout the two Americas. In this connection I follow Scudder, Poulton, and other recent authors in regarding *D. erippus*, Cram., the predominant form in the eastern and southern portions of South America, as a geographical race of *D. plexippus*, though it is separated as a distinct species by Haensch (Seitz, Macro-Lep., America, p. 113).

Throughout the whole of the warmer parts of North America we find the butterfly generally distributed and often very abundant. Its range extends southward through the West Indies and Central America beyond the Isthmus of Panama, and northward into the Dominion of Canada as far as Moose Fort at the south end of Hudson's Bay in lat. 50° 20′ N. (J. Jenner Weir, Entom., Vol. XVIII, p. 51), and according to Dr. Scudder (l.c., p. 728), still further north to the Athabasca country in about lat. 58°. It is, however, more than probable that in these remote northern localities it is not a resident species, but a migratory straggler. On the Pacific coast it reaches at least as far north as Vancouver Island, where it is no doubt resident, although I did not have the good fortune to see it when I was there in 1882. In South America its range extends southward from the Isthmus to the estuary of the Rio de la Plata, where, at Monte Video, I saw it commonly in 1880, and, on the authority of Berg (Scudder, l.c., p. 728), through Southern Argentina into Patagonia. On the western side of the continent, where it assumes the form *nigrippus*, Haensch (Seitz, l.c., p. 113), characterised by having the fulvous subapical spots in the fore-wings replaced by white, it appears to stop short at Southern Peru, being for some unaccountable reason absent from Chili. Finally, the stormy winds of the South Atlantic have in one instance at least carried the southern representative of *D. plexippus* as far as the Falkland Islands, in lat. 52° S, long. 69° W. In the " Proceedings of the South London Entomological Society " for May 26th, 1892, we read that " Mr. J. Jenner Weir exhibited a specimen of *Anosia plexippus*, L., var. *erippus*, Cramer, which had been obtained by one of the employés of Captain Parke in the Falkland Islands . . . . During Captain Parke's residence in these islands for about twenty years he had never seen a specimen of the *Anosia* in question; it therefore appears that, like its northern representative, the true *Anosia plexippus*, the southern form had the migratory habit similarly developed."

Taking the interval between the extreme northern and southern points at which it has been observed, it will be seen that *Danaida plexippus* has the wonderful range in latitude of over 110°. This is at least as great as that of the cosmopolitan *Pyrameis cardui*, whose range extends as far north as, and perhaps beyond, the Arctic Circle, its limits to the south being New Zealand and Tasmania.

Observations of Danaida plexippus and other Insects at Sea.

The observations on insects alighting on ships in the open ocean, commencing with the classical instance recorded by Darwin (Naturalists' Voyage, ed. 1901, p. 158) of a large grasshopper or locust which flew on board the " Beagle " when 370 miles from the African coast, are too numerous for quotation, but I venture to give here my own experiences in this respect. On the outward voyage of H.M.S. " Kingfisher " in 1880, in about lat. 44° N., long. 23° 30′ W., my diary notes—" a *Sphinx convolvuli* seen flying wildly and strongly about the ship," the nearest islands to windward being Graciosa and

Terceira in the Azores, each distant fully 350 miles. A few days afterwards, in lat. 6° N., long. 27° W., at a distance of 720 miles from the nearest point of the coast of Africa, I saw a butterfly on board which I failed to secure, but which was almost certainly the type-form of *Danaida chrysippus*, L.—the only alternative being *Hypolimnas misippus*, L. ♀—neither of which I had observed at the last port we had left, S. Vincente in the Cape Verde Islands.* On approaching Monte Video, in a part of the South Atlantic where this phenomenon was observed as long ago as Cook's first voyage in 1768 (*cf.* Journal of Sir J. Banks, pp. 44–45), and on many occasions since, quite a number of moths of small or moderate size and mostly in good condition came on board the ship, we being then some 120 miles from the coast. Lastly, when on a voyage from San Francisco to Callao in 1882, a fine specimen of the well-known large Noctuid moth *Erebus odora*, L. (now in the Oxford University Museum) was taken in lat. 12° 30′ N., long. 106° W., more than 250 miles from the coast of Central America, from whence alone it could have come.

The records of the appearance of *Danaida plexippus* over the open ocean in many cases at a distance of hundreds of miles from the nearest land, are of especial importance as bearing upon the question of its vastly extended distribution in recent years. I have already alluded to the records by Mathew (Ent. Mo. Mag., vol. XXII, p. 221) and by Scudder (*ante*, p. 187) of its occurrence, presumably on migratory flight, over wide stretches of the Pacific Ocean. Similar observations from the Atlantic Ocean are by no means wanting, and are, if possible, of even greater interest; some of these records may be quoted more or less in detail.

In the "Canadian Entomologist" for July, 1880 (vol. XII, p. 137), Mr. G. J. Bowles writes of one of these captures at sea—"Its powers of flight will hardly be doubted by any one who has attempted to catch it on the wing. But a stronger proof some of you have had in the exhibition of a *D. Archippus* some years ago by Mr. Pearson of Montreal, which had been captured on board a ship in the Atlantic, hundreds of miles from land." Mr. J. E. Robson in the "Young Naturalist" for 1887 (vol. VIII, p. 118) states as follows:—"I often have butterflies and other insects brought to me by seafaring friends, some of whom take the trouble to mark the latitude and longitude where the specimens were taken, or the distance from the nearest land. In the course of the last ten years several examples of this handsome butterfly have been so brought to me, one being marked 600 miles from Cape Race,* the nearest land! The specimen is in good condition, being only slightly rubbed in one place, probably by the fingers of the captor, unused to handling such fragile creatures."

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* In June, 1893, I again saw one or other of these butterflies on board H.M.S. "Tyne" in the Indian Ocean about 150 miles S.E. of Cape Guardafui, which had probably been carried out to sea by the strong south-west monsoon prevalent at the time.

In our own pages we have the record by Mr. G. A. Harker (Ent. Mo. Mag., vol. XXIX, p. 86) of the capture of a specimen some years previous to 1893, off the coast of Portugal, sixty miles from Cape St. Vincent—a position from which a flight of two or three hours at most would have brought the insect safely to land. Still more interesting is Mr. C. G. Barrett's record in the same volume (p. 163) of "several specimens of *D. Archippus* of the North American type" having been taken about the year 1880 on a vessel bound from Glasgow to New York, "upon the Atlantic, at a distance of from 200 to 300 miles from the British shores." Mr. Barrett continues—"There can, I think be no doubt, that these were a portion of a migratory swarm on its way here. Yet it is curious that no specimens appear to have been seen in Ireland." For myself, I think we have here a clear case in which a number of these butterflies had almost completed their perilous voyage across the Atlantic to our shores, when an observer on an *outward-bound* ship had the good fortune to encounter them.

The last observation to which I shall refer, by Mr. G. F. Mathew (Entom. Rec., vol. XV, p. 162), is also of very great interest, as being the sole record of *Danaida plexippus* from the Mediterranean region—"While looking through my journal for notes . . . . I came across the following, which was written on November 8th, 1897, while we were steaming through the Grecian Archipelago. I intended to send a note of it to one of the entomological magazines at the time, but did not do so. The entry reads, '*Anosia plexippus.*—One of these butterflies flapped slowly over the ship, not more than ten yards above my head, and I had a good view of it, and feel confident it was this species, with which I am well acquainted. The day was bright, hot, and calm. When I was in the Pacific, between 1881–4, I often saw these butterflies passing over, or flying about, the ship, when we were miles from any land, so I do not think it likely I was mistaken. But where can this one have come from, the east or west?'"

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* Mr. A. H. Swinton kindly informs that in 1909 he received a specimen of *Danaida plexippus* taken by his nephew at Cape Race. I do not think that the butterfly has been as yet recorded from Newfoundland.

THE "MEANS OF DISPERSAL" OF DANAIDA PLEXIPPUS.

We now come to the consideration of the agencies by means of which our butterfly has been enabled to accomplish its voyages across the ocean, and in so many cases to found successful and flourishing colonies in regions far remote from its present head-quarters. This subject was discussed by Mr. W. L. Distant in a very able and interesting paper entitled "The Geographical Distribution of *Danais Archippus*" (Trans. Ent. Soc. Lond., 1877, pp. 93–104), not long after the wanderings of the insect had begun to attract the attention of entomologists.

Like myself, Mr. Distant is strongly disposed to believe that it is quite within the power of *Danaida plexippus*, aided by favourable circumstances of wind and weather, to cross even the wider parts of the great oceans. He writes (l.c., p. 95): "That the winds alone are a great agency of dispersal with the *Lepidoptera* cannot be doubted with the number of authentic records we have of butterflies and moths being found far at sea and great distances from the nearest land; and it will readily be understood that butterflies of high and strong flight, especially when at certain seasons they become gregarious, must have a greater chance of being borne on the wings of a strong wind or carried away by a sudden gale than those insects whose flight is low, or whose habits are more solitary and secluded. Now we know that *D. Archippus* has a powerful flight, often sailing with wings expanded high in the air . . . . We also learn from Mr. Riley that the butterfly appears in large bevies or flocks almost every year in some part or other of the west . . . . Mr. Riley further remarks, 'this assembling in large flocks at a considerable height would always be a source of danger to them, when overtaken by a gale of wind, when there would be a great probability of their being carried out to sea' . . . . Winds alone can scarcely be considered the only cause of the migration of butterflies over large areas of sea, though of the highest efficacy for the purpose. When met with far away from land they seem glad to alight on the vessel for rest, and no doubt vast numbers must succumb to the waves; for apart from the vigour required to sustain such a long flight, the spray in rough weather would sufficiently damp their wings to prevent any onward progress, and very rarely would one be able to survive the long flight across the breadth of the ocean."

Whatever might be the fate of the butterfly attempting to alight on the surface of the sea when at all rough, the following observation by Dr. Seitz (Macro-Lep., Palæarctic Region, I, p. 77), "I very often saw *plexippus* at sea flying at a very considerable height, and observed that it could settle on the surface of the water with the wings expanded and rise again without difficulty into the air," would suggest that not only is it quite able to do so with safety in calm weather, but that it might even be able thus to obtain a certain amount of needful rest. It is evident that a rest of this kind might be of material assistance to a migrating butterfly in effecting a long sea passage.

Dr. Scudder is not disposed, however, to admit of the butterfly being able, by its unaided flight, to cross more than a moderate extent of ocean. I give here his views in full (l.c. pp. 733, *et seq.*) :—

"I have spoken of the extension of its natural region as one due to commercial agencies, because it would seem that the distance to which the insect has been carried must be due to something more than its very remarkable powers of flight. The fact that the butterfly has been seen flying at sea five hundred miles from land is a sufficient proof of the latter, and we should be far from questioning its power to compass with no very great difficulty one-half the extreme distances to which we know it has been carried without power of alighting. But that this should occur with a female heavy with eggs (and no other supposition would permit us to understand its subsequent propagation in the regions visited) is past credence; more especially as we have in the instance of its transport from the Hawaiian Islands to the Caroline group an almost certain proof of the method of its transport, through artificial aid. The alighting of one of these butterflies laden with fertile eggs, upon some part of a vessel or within its hold would by no means be a strange occurrence, and this is all that is necessary to explain its transport over the wider regions. That having once established itself in the Micronesian Islands it could easily spread over the whole of Polynesia through the insect's ordinary powers of flight, will not be questioned. But that this has taken place not only within historic times, but within the last twenty or thirty years, as has been shown by Semper, is an almost direct proof that its first introduction to the South Seas was by artificial means; for if it could be brought about solely by the power of flight of the insect, aided by the natural currents of the air, it would have happened long ago, and the fact that the insect has been able to establish itself wherever it chose when it got a foot-hold, and that it has not until a recent period established itself, are sufficient proofs that commercial agencies, so much more abundant in later times than formerly, have been the great means of introducing these butterflies to the islands of the Pacific. It is highly probable that it owed its first introduction to the Hawaiian Islands to similar agencies, and that its appearance in Europe is due to the same cause."

As far as I am aware, we have no proof of the "æstivation" of this, or indeed of any butterfly, and I much doubt the probability of the perfect insect remaining quiescent on or in any part of a ship in the tropical regions, as suggested above by Dr. Scudder. In a voyage of any length, too, it would be always exposed to the risk of being sooner or later blown away from the vessel. Darwin (l.c., p. 158, foot-note) writes, "The flies which frequently accompany a ship for some days on its passage from harbour to harbour wandering from the vessel, are soon lost, and all disappear." On the other hand, a ship in mid-ocean may well form as welcome a resting-place for a wandering butterfly as for a migrating bird, and may be at times the means of enabling either to reach a new land.

The probability of *Danaida plexippus* being transported in its early stages is, I think, even less than in the case of the imago. In the warmer parts of its range, the whole of its transformations, from the laying of the egg to the emergence of the perfect insect, are effected in six weeks or even less (Ent. Mo. Mag., vol. XXII, p. 218), the eggs hatching in from four or five days to a week, and the pupa state lasting two or three weeks at most. Thus in the event of the pupa (*cf.* Seitz, Macro-Lep., Pal. Region, I, p. 77, footnote), or even the food-plant with eggs attached, having been included in "bales of hay" these eggs would stand a very small chance of remaining unhatched on a sea voyage of any length, and the young larvæ would almost inevitably perish. The integuments of the larva, unlike those of the imago, are very soft and tender, and readily liable to mechanical injury. Again, no one who has ever handled a living pupa or the filmy transparent shell of one that has been vacated by the perfect insect, will be likely to admit the possibility of its surviving the rough treatment it would necessarily receive if included by accident with merchandise on board ship. This also appears to me to dispose of the suggestion by Mr. Distant (l.c., pp. 97–8) as to the possibility of the butterfly, in any of its stages, being conveyed to distant lands by the agency of trees or other "natural débris" borne on the great currents of the ocean, however efficacious such means may be in the case of other creatures of a more hardy nature.

From my further experience of *Danaida plexippus*, I see no reason whatever to modify the opinion expressed in my former paper in this

Magazine (l.c., p. 222) as to its ability to traverse the spaces of ocean that divide its American home from the nearest lands east and west, by means of its own good wings, with no other assistance than the favour of the elements. To begin with, its flight, if not as rapid as that of many other butterflies, is powerful, sustained, and untiring; its habit of assembling in great swarms, and of mounting high in air, have been alluded to by every writer on its life-history; and finally, the toughness of its integuments, as well as its hardiness, vitality, and longevity, are exceptional even for the highly protected family to which it belongs. Thus everything is in favour of some individuals at least of a swarm of these butterflies, blown by a heavy gale out to sea and probably carried up to a great height by ascending air-currents, surviving for days, if not for weeks, and eventually "making the land," as indeed was so nearly the case with those recorded from the Atlantic by Mr. Barrett (*ante*, p. 231). Borne on the wings of the wind, with no more exertion than would be necessary to enable them to keep their balance, they would incur very little if any damage or "waste of tissue," and on their arrival at a foreign shore, even a "female heavy with eggs" would no doubt be in sufficiently good case to found a colony, provided always that the necessary food-plant were at hand.

As it is, to say the least, very unlikely that the insect under these circumstances would be accompanied by any one of its very few parasites or other enemies, its rapid increase in many of its new homes is readily accounted for. This increase would not be checked, except as in New Caledonia by the wholesale destruction of the food-plant by the larva (*ante*, p. 190), or as at Sydney (Ent. Mo. Mag., vol. XLI, p. 220) by one or other of the local parasitic insects finding out and adapting itself to the new-comer.

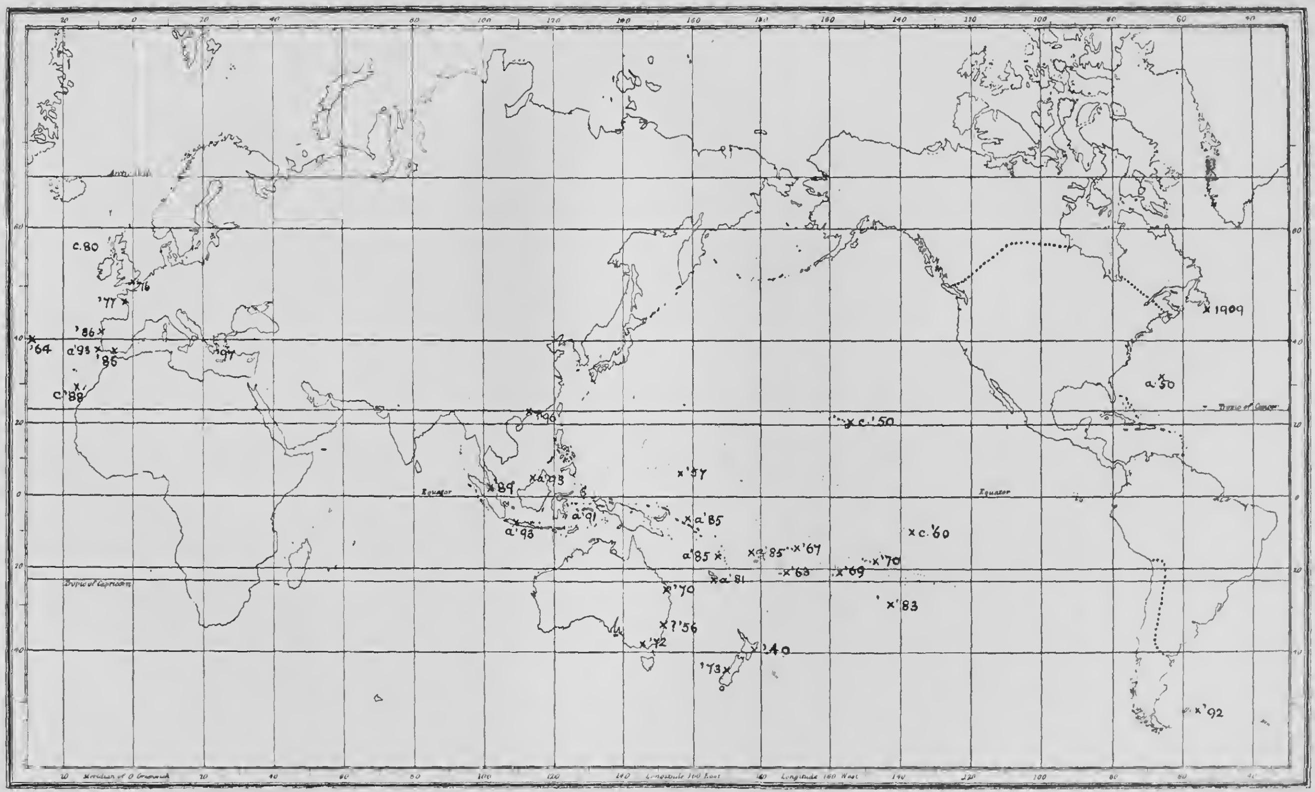
It is the arrival of the food-plant before that of the butterfly that, in my opinion, is the determining factor of the ability of the latter to establish itself in any new region. In every locality where it has been noted as more than a casual visitor, it will, I think, be found that either *Asclepias* or *Gomphocarpus* has arrived there before it. Now both these plants, although troublesome weeds to tropical cultivation and possessed of decidedly poisonous properties, are sufficiently ornamental to cause them to be sometimes grown as garden flowers or curiosities, and thus they may in some cases be deliberately introduced into new localities, as *Gomphocarpus* has been into New Zealand and the Azores. As regards *Asclepias curassavica*, it is not easy to fix even an approximate date for its introduction into the Pacific Islands; but the fact quoted by Mr. Distant from B. Seemann's "Flora Vitiensis," p. 161 (1865–73) that it had been recorded from Eromanga, the New Hebrides, and the Tongan and Society groups, "probably introduced as not known to the older botanists," seems to show beyond doubt that it was there at that time awaiting the arrival of the butterfly. Besides the introduction of the plant by man, intentional or otherwise (as in the case of New Caledonia, *ante*, p. 189), it is in itself eminently adapted for dispersal by natural agencies alone. The seeds are very minute, and enveloped in a mass of silky down or cotton of the finest and lightest texture, capable of being blown, if not across the entire width of the great oceans, still for hundreds of miles before the strong and steady breezes of the intertropical regions. In one way and another *Asclepias curassavica* has already nearly completed the circuit of the globe, if indeed it has not already done so.

Thus it would appear that human agency has played not a primary, but at most a secondary part in the dispersal of *Danaida plexippus*. Many a time since the butterfly became established in North America —possibly soon after the glacial epoch—individuals or small companies have been carried with the aid of the winds to far distant lands, but these pioneers, failing to find suitable food for their progeny, have perished without continuing their race. With the great increase of communication with the Pacific Islands and coasts which commenced before the middle of the last century, this deficiency has been supplied, and we now find *Danaida plexippus* ranging over a greater extent of the earth's surface than any other butterfly, with one possible exception. Probably, too, it is only a question of a few years before vast areas in Asia and Africa, to all appearance as suitable to its existence as those it has already occupied, will be colonized by this bold and enterprising insect.

With regard to the probability or otherwise of our butterfly becoming established in Europe, I have personally no doubt as to its finding, on the shores of the Mediterranean, a climate and environment eminently suited to its requirements, in the event of its reaching that region under favourable conditions at any future time. Even if *Asclepias curassavica*, which, as we have already seen (*ante*, p. 193), had more than twenty years ago spread as far as the Suez Canal, should from any cause fail to obtain a footing farther westward, an acceptable food-plant is available in the closely allied *Gomphocarpus fruticosus*. This plant, widely distributed in Africa, is also found in Syria and Asia Minor, and I saw it many years ago growing freely in the region of the Dardanelles. Of the other European members of the same Natural Order, *Periploca græca*, L., extends throughout the Mediterranean region as far west as the Rock of Gibraltar, and *Vincetoxicum officinale*, Moench, is found throughout the warmer parts of the Continent, reaching as far north as Denmark and Sweden. As, moreover, according to Saunders (Scudder, l.c. p. 737), the larva has been discovered on *Apocynum androsæmifolium*, L., it is quite possible that the well-known *Nerium oleander*, and the "periwinkles," *Vinca major* and *V. minor*, also members of the Natural Order *Apocynaceæ*, would not be refused. In captivity at any rate the larva appears to adapt itself to an even more unlikely pabulum. Dr. Seitz states (Macro-Lep. Pal. Region, I, p. 76), "I have always found the larva at large on *Asclepias*, but young caught caterpillars accept as food also lettuce, thriving very well on such food." It is in the highest degree improbable, though, that the insect would take to this food of its own free will. Although both the above-mentioned species of *Vinca* are common enough in the South of England, I greatly fear that the capricious nature of our climate, especially as regards summer temperature, will effectually prevent the establishment of *Danaida plexippus* as a resident in our Islands.

In the accompanying sketch-map I have endeavoured to mark the progress of *Danaida plexippus* across the oceans, by means of the dates on which it was first recorded from the stations (marked with a small cross) mentioned in the preceding pages of this paper. The figures indicating the century are omitted, and the approximate limits of the range of the butterfly in North and South America are shown by dotted lines.

Aorangi, Lonsdale Road,
Summertown, Oxford:
August, 1914.



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Sketch-map showing Distribution of Danaida plexippus.

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ON THE OCCASIONAL OCCURRENCE OF BUTTERFLIES IN ICELAND; WITH NOTES ON THE LEPIDOPTEROUS FAUNA OF THE NORTH ATLANTIC ISLANDS.

BY JAMES J. WALKER, M.A., R.N., F.L.S.

The question as to the occurrence of any indigenous species of *Rhopalocera* in Iceland has for a long time formed a subject of discussion with those entomologists who are interested in the geographical distribution of insects. At first sight it would appear highly improbable that an island considerably larger than Ireland, lying within the influence of the Gulf Stream and thus possessing a climate much less severe than that due to its high latitude, can be entirely destitute of butterflies, several species of which are well known to extend their range to the northernmost limits of land. But all available evidence hitherto appears to show that no really native butterfly is found in Iceland, with possibly one exception to be referred to hereafter; and that most, if not all, the butterflies that have been observed within its limits are wanderers from more genial regions which have successfully braved the dangers of the stormy North Atlantic Ocean.

It is true that a great part of the interior of Iceland is altogether unsuited to insect life, consisting as it does of ice-covered mountain slopes, extensive fields of naked lava, and vast stretches of loose volcanic sand, all equally destitute of vegetation of any kind. Many parts of the island, however, especially in the north, are comparatively fertile and luxuriant, and can even boast of what may be called miniature forests of sallow, willow, and birch, the latter tree sometimes attaining a height of twenty feet or more. The Icelandic flora, too, is fairly rich, as, according to Dr. Lauder Lindsay (Edinburgh New Philos. Journal, new series, vol. xiv, pp. 64–101), it comprises no fewer than 426 species of flowering plants. These conditions would appear to indicate the presence of at least a moderately extensive Lepidopterous fauna, which is not borne out by the results of such researches as have been made so far, and Iceland, in this respect, is probably one of the poorest regions of the whole earth. It must be remembered, however, that no equally accessible land of the same extent has been so inadequately explored from an entomological point of view. So far as I am aware, Iceland has never produced a single resident collector or observer of insects, and such knowledge of the subject as we possess is due to a very few of the numerous summer visitors from Europe—above all, to the late Dr. Staudinger, whose classical paper on the results of his expedition in 1856 ("Reise nach Island": Stett. Ent. Zeitung, 18 Jahrgang, 1857, pp. 209–289) still remains the most important single work on the insect fauna of this great island.

The oldest record of Icelandic insects by N. Mohr ("Forsög til in Islands Naturhistorie": Kjöbenhavn, 1786) includes 12 species of Lepidoptera; and the same number of species appears in a list of insects compiled by M. Paul Gaimard in the Appendix to the official narrative of the voyage of the French corvette "La Recherche" to Iceland and Greenland in 1835–6. This list is reproduced in Dr. C. W. Paijkull's well-known work "Ein Sommer in Island" (English translation, 1868, pp. 355–6). Like the last, it mentions no butterflies, and is otherwise of not much value. In the "Table of Distribution" of the very useful little "Manual of European Butterflies" by the late W. F. Kirby, the following species are ascribed to Iceland—*Colias palaeno* L., *C. phicomone* Esp., and *Chionobas oeno* Bdv. (Boisduval); *Colias hecla* L. (Linné), *Chionobas jutta* Hb., and *Argynnis freyja* Thnb. (De Villiers et Guenée). From the known distribution of these species, it is very unlikely that any of them can occur in Iceland, and, as far as I am aware, no specimens exist in any collection, with the possible exception of the last-named butterfly, the case for whose occurrence in Iceland will be considered later on.

The expedition of Dr. Staudinger, who was accompanied by C. Kalitsch, an excellent practical collector, occupied most of the summer of 1856, from May 18th to the middle of September. His researches were chiefly made in the relatively barren south-western portion of the island, but fortunately another experienced entomologist, Dr. Krüper, spent most of June and all July of the same year in the much more luxuriant region round the lake Myvatn in the north-east. Some insects were also collected in the same year by Herr Finsterwalder on the north coast, in the Siglufjordr region, which was, however, found to be very unproductive. The whole of the insects obtained by these entomologists are included in Dr. Staudinger's paper, in which 311 species in all are enumerated. Of this number 110 belong to the *Diptera*, 81 to *Coleoptera*, and 66 to *Hymenoptera*; the *Lepidoptera* comprising only 33 species, little more than one-tenth of the whole, and the remaining Orders being even more poorly represented; *Orthoptera*, indeed, being apparently totally unknown in Iceland. Respecting the *Lepidoptera*, Dr. Staudinger (*l. c.* p. 229) writes as follows:—"The 33 species found by us belong to the Noctuae, Geometrae, and Micro-Lepidoptera—*Papilionidae*, *Sphingidae*, and *Bombyces* are altogether absent. . . . . The absence of *Papilionidae* and *Bombyces* is more surprising (than that of the *Sphingidae*). Indeed, some authors mention Diurnal Lepidoptera as occurring in Iceland, but I must decidedly contradict these statements. In my opinion it is not possible for butterflies to live in Iceland, and should they have existed in former times they must have perished. The situation of Iceland has nothing to do with it, as Diurnal Lepidoptera are known to occur much farther north. To find the reason in the volcanic devastations is very artificial, always hypothetical only, and can be refuted by the facts." He goes on to suggest that the constant rain, the stormy weather, and usually low temperature of summer, as well as the general absence of shelter, are the causes which militate against the occurrence of butterflies in Iceland.

In the summer of 1889 Iceland was visited by two well-known English entomologists, Dr. Philip B. Mason and the Rev. Francis Walker, D.D. The researches of Dr. Mason (Ent. Mo. Mag. vol. xxvi, pp. 198–201) were confined to the rather poor region near Reykjavik and the Geysirs in the south-west, but Dr. Walker (Entomologist, vol. xxii, pp. 222–25, 246–49, 273–75, 299–302), besides collecting at these places, landed at no fewer than fifteen fjords in the course of a coasting voyage round the island, and obtained insects at most of them. Although a good many Lepidoptera, including some species not included in Staudinger's list, were met with by these travellers, no butterfly of any kind was observed by either, though Dr. Walker remarks (*l. c.* p. 222): "Some of the days occupied in riding were so fine and hot, that had there been any butterflies at all in the (south-west) district, I feel sure that I should have seen them." But he also states (*l. c.* p. 222) that Dr. Jon Thoroddsen, the well-known Icelandic geologist and traveller, informed him that he had observed a single specimen of *Pyrameis cardui* in Shore Street, Reykjavik, in the previous summer. This appears to be the first reliable record of the occurrence of any butterfly in Iceland.

Dr. N. Annandale, in his very interesting little work "The Faroes and Iceland," published in 1905, remarks (p. 214): "Butterflies do not exist as natives of Iceland and the Faroes; but a specimen of the Painted Lady has been recorded from the Faroes, and several species apparently visit Iceland as occasional immigrants from Greenland, though I do not know that any have actually been recorded. There are specimens, said to have been caught in Iceland, in the Natural History Museum at Reykjavik, and they probably belong to a species of Fritillary which is well known as an Arctic form." Quite recently Dr. Annandale has informed me that this "Fritillary" is one of the smaller kinds, probably one of the circumpolar species of *Brenthis*, and it may even be the *B. freyja* reported by Kirby to occur in Iceland on the authority of De Villiers and Guenée. Without seeing the specimens, however, it is impossible to say with certainty what the insect really is; but I very much doubt whether any of the few species of butterflies that occur in East Greenland, none of which are known to be migrants, can be able to cross the 250 miles of more or less ice-encumbered sea which separates that country from Iceland.

The latest paper that I can find which deals with the subject of Icelandic Lepidoptera is one by Dr. C. Aurivillius (Arkiv för Zoologi, Band 8, No. 12, pp. 15–17), treating of the insects of that Order met with by Dr. Axel Freiherr von Klinckowstrom in Iceland and the Faeroe Islands in 1909–10. One or two species are added to the list of those already known from the former island, but again there is no mention of the occurrence of any butterfly.

Quite recently, through the kind offices of the Rev. Dr. Skat-Hoffmeyer, of Copenhagen, I have been placed in communication with Dr. Bjarni Saemundsson, the Curator of the Natural History Museum of Reykjavik, who has very courteously given me particulars of the following *Lepidoptera* now in the Museum:—

"*Vanessa atalanta*. One, taken in Reykjavik, June 15th, 1901.

"*V. cardui*. Five specimens taken near Reykjavik, July 1894, B. Gröndal; and one specimen (very fine) also near Reykjavik, October 14th, 1914.

"*Sphinx convolvuli*. One or more specimens, in very poor condition, from the neighbourhood of Reykjavik.

"One specimen taken at Hvanneyri in Borgarfjord, South-west Iceland, in the spring of 1916 by Mr. Halldór Vilhjálmsson.

"One specimen taken in Reydarfjord, South-east Iceland, in September 1899, by Mr. Lára Olafsson."

Dr. Saemundsson also remarks that "now and then people are seeing butterflies, sometimes in great numbers, without catching them, e. g. *Vanessa atalanta* (of which we have one specimen in the Museum) and maybe some of them are *V. cardui.* Otherwise butterflies are not citizens of our Fauna, only occasional visitors." I am indebted to his kindness for specimens of *Pyrameis cardui* and *Agrius convolvuli*, both in very travel-worn condition; these I have deposited in the Hope Department of the Oxford University Museum.

Thus it would appear that Iceland is occasionally visited by at least three species of *Lepidoptera*, notorious for their migratory propensities, and possessed of powers of flight sufficient to carry them across the most stormy tract of the ocean in the Northern Hemisphere. All three are well-known visitors to the Shetland Islands at not infrequent intervals, and one of them, *Pyrameis cardui*, has been recorded by Hansen from the Faeroes as long ago as 1881. *Plusia gamma*, its frequent companion on migration, which was not observed by Dr. Staudinger in Iceland, was taken at Reykjavik by Dr. Nordenskiold's expedition in 1883, and by Dr. Mason and Dr. Walker on their visit to the island in 1889; it was also taken by von Klinckowstrom, who records it from the Faeroes as well. Whether *Pyrameis atalanta* or *P. cardui* may be able to perpetuate its kind in one of the warm and genial summers with which Iceland is sometimes favoured, is open to question; but the capture of the latter butterfly in fine condition in October leads one to speculate as to whether this does not happen on rare occasions. The flora of Iceland includes four species of thistle, our two common British nettles, and the common mallow, so that either of these butterflies reaching the island would find suitable food-plants for its progeny.

It may be of some interest to compare the scanty Lepidopterous fauna of Iceland with those of the Faeroes and the Shetlands, the two nearest groups of islands in the North Atalantic. The following table is compiled from (*a*) "Distribution of Lepidoptera in the Outer Hebrides, Orkney, and Shetland," by R. South (Entom., vol. xxi, pp. 28–30 and 98–99); (*b*) "Faunula Insectorum Faeröensis," by H. G. Hansen (Naturhistorisk Tidsskrift, 3 Raekke, 13 Bind, pp. 229–278: Copenhagen, 1881); (*c*) the lists of Icelandic insects by Dr. Staudinger, Dr. Mason, Rev. F. Walker, and Dr. Aurivillius, already cited, with the addition of the species communicated to me by Dr. Saemundsson :—

Family or Division.	SHETLAND ISLANDS. Lat. 60° 30′ N. 551 sq. miles.	FAEROE ISLANDS. Lat. 62° N. 511 sq. miles.	ICELAND. Lat. 63° 30′ N.–66° 30′ N. 40,437 sq. miles.
Rhopalocera ...	5	1	?3
Sphingidae... ..	2	—	1
Arctiidae	1	—	—
Noctuina	37	7	10
Geometrina ...	13	4	12
Pyralidina	7	1	—
Crambina	5	—	3
Pterophorina ...	—	—	1
Tortricina	17	—	4
Tineina	9	2	11
Hepialidae	2	1	—
Total	98	16	45

To the three species of butterflies noted by Mr. South as occurring in Shetland may be added *Euvanessa antiopa*, recorded by Mr. J. J. F. X. King (Ent. Mo. Mag., vol. xxxvii, p. 226) as having been seen by him, but not captured, in the island of Unst on August 15th, 1901; and my friend Mr. G. Claridge Druce, the eminent botanist, who is well acquainted with our butterflies, assures me that he caught a specimen of *Aricia astrarche* var. *artaxerxes* in the same island in July 1920. *Coenonympha typhon*, which appears to be scarce, is probably the only species really indigenous to Shetland.

With the single exception of *Hadena sommeri* Lef., also common in Iceland, all the *Lepidoptera* as yet recorded from the Faeroes occur in Shetland. Perhaps the most noteworthy species is *Hepialus humuli*, the Faeroese specimens of which closely resemble in both sexes the lighter-coloured forms of the var. *hethlandica* Staud., the males especially being intermediate between that variety and the white type-form. Dr. Annandale states ("The Faroes and Iceland," p. 215) that "the Ghost Moth sometimes appears in great numbers in the Faroes at the end of July and the beginning of August," and the Oxford University Museum possesses a fine series taken by him in the island of Boro in July 1900.

As might have been expected from the generally wide distribution of Arctic forms, the majority of the Iceland *Lepidoptera* are of species also found in Northern and Central Europe, with a very slight element of more southern character, for instance as *Triphaena pronuba* L., recorded by Dr. Staudinger and Dr. Mason. The entire absence of the characteristic Arctic genus *Anarta* is especially noteworthy, and is attributed by Dr. Staudinger to the usually unsuitable weather for these sun-loving insects. Only three well-defined species appear to be peculiar to Iceland: *Melanippe thulearia* Staud., allied to our *M. hastata*; *Crambus extinctellus* Zell., near *C. pascuellus*, but probably distinct; and *Pterophorus* (*Stenoptilia*) *islandicus* Staud., a well-marked form. Certain other species, such as *Hadena* (*Crymodes*) *exulis* (perhaps the most characteristic moth of Iceland), *Mamestra pisi*, *Cidaria truncata*, *C. immanata*, *C. munitata*, *C. designata*, *Eupithecia sobrinata*, and *E. valerianata*, present remarkable phases of variation, some which are altogether confined to the island.

There being no true night on Iceland during most of the summer months, the *Lepidoptera* may be found on the wing throughout the whole twenty-four hours, the flowers most favoured by them, according to Dr. Staudinger, being *Spiraea ulmaria*, *Silene acaulis* and *maritima*, and *Thymus serpyllum*, all of which, especially the last, grow in profusion throughout the island. Although the species are so few in number, many non-entomological travellers have been strongly impressed by the enormous numbers of individuals met with in favourable seasons and situations. And Dr. Walker remarks (Entom. vol. xxvi, p. 223):—"As though to make up for the total absence of diurnal *Lepidoptera*, the quantity of certain species of moths is something astonishing. I do not recollect ever having seen Geometridae so abundant elsewhere—rising in a cloud from the scrub vegetation when the dwarf willow or birch was lashed by the riding-whip of our guide, on the grassy slopes of the mountains, and likewise on the meadows adjoining the homestead—everywhere most numerous." A larva, in all probability that of *Episema* (*Charaeas*) *graminis*, is reported to work great havoc in the pasture-lands and hayfields, in certain years, just as is the case with the same species in Britain.

As it is doubtful whether the estimate of Dr. Staudinger, made nearly seventy years ago, of a maximum number of 500 indigenous species of insects of all Orders, has up to now been exceeded or even attained, it is evident that Iceland holds out but few inducements to the entomologist, except perhaps the chance that a truly native butterfly may at some future time be found in one or other of its sequestered valleys.

Aorangi, Lonsdale Road, Summertown, Oxford.
December 16*th*, 1921.

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NOTES OF A VOYAGE TO AUSTRALIA, CEYLON, AND THE MALAY ARCHIPELAGO, JULY—NOVEMBER, 1914.

BY F. A. DIXEY, M.A., M.D., F.R.S.

Gibraltar was reached on July 7th. Very few insects were seen; a hot walk up the slopes at the back of the town resulted only in the capture of *Ganoris rapae* Linn., ♀; a wasp, *Polistes gallicus* Linn., ♀; and a bee, *Halictus* sp., ♀. *Colias edusa* Fabr. was seen, but not taken. The Alameda, or public garden, displayed a wealth of brilliant flowers: oleanders, *Hibiscus*, *Ipomoea*, *Plumbago*, and tree-geraniums. Here, however, no butterflies were observed except a few more specimens of *G. rapae*, and the only other insect secured was the fine long-waisted wasp, *Sceliphron spinifex* Linn., ♀. Some members of the landing party encountered one of the monkeys that inhabit the rock. The unfortunate animal was being stoned by a number of men from the town. Our friends interfered, and the monkey made his escape.

In the Suez Canal, on July 16th, *Danaida chrysippus* Linn. was observed flying close to the ship; and in the Red Sea, on the following day, a rather worn *Pyrameis cardui* Linn. came on board.

The next entomological event of the voyage took place on July 19th, in the Gulf of Aden. Here a swarm of locusts invaded us at about 8 p.m., dispersing themselves over the decks, thronging the gangways, making their way into the state rooms, and causing much annoyance by clinging to the clothes and hair of the passengers. Members of this aerial raid continued for some days afterwards to turn up in the most unexpected quarters. The species was *Schistocerca peregrina* Oliv. It is a beautiful insect, creamy pink in colour, with the forewings prettily mottled. The expanse of wing in an average specimen is fully five inches. It may be noted that those specimens observed in 1905 by Dr. Longstaff and myself in South Africa, were of a much darker colour, their hue being perhaps best described as mahogany red.

On July 25th we had a day ashore at Colombo. In the early morning the rain came down in torrents, but this soon cleared off and the heat became intense. I walked southwards along the sea-front, admiring the immense breakers raised by the S.W. monsoon which we had experienced on the way from Aden. At Galle Face, where there is a picturesque grove of coco-nut palms on the very verge of the sea, I turned inland and continued my walk along the side of a lagoon edged with palm trees and reflecting the lines of a Buddhist Temple. The shallows were thronged with water-tortoises, which sank as one approached. Impudent crows were everywhere, looking out keenly for anything dropped. Halting beside an enclosure between the lagoon and the beach, I made a few captures. They would have been more numerous but for the tiresome attentions of importunate natives, mostly children.

Dragon-flies, especially *Brachythemis contaminata* Fabr., were abundant, as also were great dark-blue bees of the genus *Xylocopa*; one brought home is *X. fenestrata* Linn. ♂. *Terias hecabe* Linn. was present in large numbers; the only one taken is a wet-season male. *Telchinia violaë* Fabr. was fairly common; two males had a slight odour of straw, in two others no scent was detected. Many males of *Hypolimnas bolina* Linn. were observed; no female put in an appearance. *Catopsilia pyranthe* Linn. frequented the sunny sides of the enclosure. The males were noted to possess a strong odour like that of jasmine. In one of these, a somewhat worn specimen, the scent was easily perceptible on the following day, when the observation was confirmed by a lady fellow-passenger. A somewhat ragged male of *Zizera gaika* Trim., noted as "odourless," and a small green Hemipteron completed the bag.

On July 30th we passed the Cocos or Keeling Islands. The Commander of R.M.S. *Orvieto* obligingly brought the ship in near enough for us to see men on the beach, and to appreciate the striking contrast between the blue waters of the outer ocean and the vivid green expanse within the encircling coral-reef. A white-sailed yacht made its way slowly across the calm lagoon, and with the yellow sands and verdant palm-trees of the island shores, made a charming picture. We little thought that this peaceful spot was shortly to become the scene of the discomfiture of the famous cruiser *Emden*, with its attendant fire and slaughter.

On August 4th we landed at Fremantle and went on by train to Perth. Here we were met by the disquieting news of the outbreak of war, the sense of which calamity was to haunt us during the rest of our journey. Embarking again at Fremantle, we steamed across the great Australian Bight, receiving on Aug. 6th, by wireless, orders to cover our lights. Neither at Adelaide (Aug. 8th–12th), nor Melbourne (Aug. 13th–19th), were insects much in evidence; but at Marysville, some 50 miles N.E. of Melbourne, a man came over on horseback to tell us that he knew of a lyre-bird's nest. A few of us started off to see it; we were led in single file through the bush. Having been told that the bird was not sitting, we naturally went up close to the nest, which was a large, round, covered-in structure, two or three feet from the ground. A lady of our party stooped to look in; there was a rush and a scramble; out flopped the lyre-bird; struggling through the scrub, it came to a small torrent, across which it flew. Alighting on the other side it ran swiftly up a fallen tree trunk on the sloping bank, and finally disappeared in the bush. The nest contained a single egg: large, smoky-brown, with a tinge of green. It was rapidly examined and carefully replaced.

At Sydney (Aug. 20th–26th) a species of *Euploea*, probably *Chanapa* (*Euploea*) *corinna* McLeay, was to be seen occasionally in the University precincts. These were the first butterflies I had met with in Australia.

At Brisbane (Aug. 27th–Sept. 3rd) matters entomological showed a decided improvement. Many butterflies, including *Papilio sarpedon* Linn. and *Precis velleda* Fabr., were to be seen in the town itself; while in the outskirts *Acraea andromache* Fabr. was abundant and *Delias nigrina* Fabr. common. The former of these two species had the slow, deliberate flight characteristic of the genus, and was often observed to settle on the ground; the latter, also with a slow flight, kept mostly out of reach, haunting the tops of trees and passing from one to another with a sailing motion that displayed the dark ground-colour and brilliant red band of the under surface.

Passing up inside the Great Barrier Reef, and within sight of some delightful-looking islands, the S.S. *Montoro* reached Townsville on September 6th. Here I spent most of the day in the scrub among the hills at the back of the beach. Butterflies were fairly numerous, but, owing to the rough nature of the ground, by no means easy to catch. *Tirumala hamata* McLeay was abundant in places, flying round trees and occasionally settling on twigs. In one male I detected a slight odour like that of old straw, and in another a faint flowery odour on detaching scales from the fold on the underside of the hindwing. *Chanapa* (*Euploea*) *corinna* McLeay was also locally abundant; two males, one of which extruded yellow tufts, were tried for scent with a negative result. Satyrids were conspicuous by their absence, but a specimen of *Yphthima arctous* Fabr. was secured. Perhaps the most striking insect seen was *Eurycus cressida* Fabr. This was fairly common, not constantly visible like the Danaines, but every now and then attracting attention by its slow flight from tree to tree. A specimen of the male sex was noted as having a distinct acrid smell. No odour was detected in a worn and rather ragged example of the female. *Terias lineata* Misk. was abundant, *T. hecabe* Linn. quite common. Two males of the latter both showed the wet-season coloration. Other captures in the scrub near Townsville were *Eumecopus armata* Fabr., a quietly-coloured but very handsome Hemipteron; and a reddish-grey immature grasshopper, at present undetermined.

On the following day (Sept. 7th) I crossed over to Magnetic Island, which lies north-east of Townsville, in Halifax Bay. Here again the roughness of the ground and the character of the undergrowth made collecting difficult, and the number of insects caught bore a somewhat slender proportion to the number of those seen.

(*To be continued.*)

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(Continued from page 13.)

Tirumala hamata was locally abundant. Its gregarious habit was especially noticeable; large numbers were seen swarming round a mango tree near the settlement. A female specimen taken showed a symmetrical injury to the two hind wings. Satyrids were plentiful; those captured included the soberly-coloured *Yphthima arctous* Fabr., a male specimen of which yielded a very distinct smell of vanilla, *Hypocista irius* Fabr., and *H. adiante* Hübn. In each of the latter species the forewings are somewhat sharply pointed for a Satyrid, and the underside of the hindwings is ornamented with a large and very conspicuous ocellus. *Y. arctous* was noted as common; *H. adiante*, which somewhat recalls our familiar " small heath," as abundant. The only Lycaenid brought away was a male specimen of *Candalides erinus* Fabr. *Eurycus cressida* Fabr. was again in evidence; a good specimen of the semi-transparent female was secured. This butterfly, from its conspicuous aspect and deliberate flight, looks as if it ought to be easy to catch. But it has a tantalising way of keeping just out of reach, and its pursuit through the thick undergrowth interspersed with loose granite blocks, which are the prevailing features of the uncultivated part of Magnetic Island, was not unattended with risk to one's ankles. Its appearance was intermittent; every now and then *cressida* would come suddenly into view, and after a short flutter would be lost to sight amid the foliage of a tree at a height just too great to be reached with the net. The male especially is a striking object; its semi-transparent forewings and the vividly contrasted red, white, and black of the densely scaled and opaque hindwings give it a character which is quite distinct from that of any other inhabitant of these regions. As before noted, the worn female captured at Townsville appeared to be scentless; but the female taken on the present occasion, which was in good condition, emitted a distinct and strong odour, noted in the field as " ammoniacal," and at home as exactly that of musk.* The same specimen was observed to be tenacious of life. An interesting capture was that of a pair of *Delias argenthona* Fabr. This species was not uncommon, and with its slow flight and bright coloration beneath, presented a conspicuous appearance. The male was tested for scent with no perceptible result. A single specimen of *Catophaga ega* Boisd., ♀ fell to the net, but no corresponding male was seen. Small yellow butterflies of the genus *Terias* abounded in the undergrowth. These belonged to two distinct groups or sections, *T. lineata* Misk., the predominant form, being a member of the assemblage represented by *T. laeta*, Boisd., while the other species present was the widely distributed *T. hecabe* Linn. Fresh specimens of the latter appeared to be generally of the dry-season form, but the wet and intermediate phases were also to be met with. A male *T. lineata* yielded a faint flowery odour in scrapings of the scent glands; in two males of *T. hecabe* a slight but distinct flowery perfume was detected. In one of these, a dry-season male, the "dog's head" was feebly developed. The delicate-looking dragonfly, *Neurothemis stigmatizans* Fabr., ♂, and an unnamed Hemipteron near *Riptortus fuscus* Fabr. completed the catch on Magnetic Island, from which place we returned in the evening to Townsville, across a sea which the sailors themselves acknowledged to be exceptionally rough.

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* In my diary for June 29th, 1890, at Port Darwin, North Australia, I find noted under the capture of *Eurycus cressida* ♀, that " this butterfly emits when caught a strong and not unpleasant odour of musk."—J.J.W.

We had expected to clear from Townsville on the evening of September 7th, but were detained by order of the Naval authorities. At 3 a.m. on the 8th we were told to dismantle our wireless apparatus and stay where we were until further notice. We were kept in uncertainty about sailing all day long, but I found it possible to go ashore for an hour or two in the afternoon and to do a little collecting in a steep and stony gully north of Townsville. The President of the British Association and Mrs. Bateson, who also landed, drew my attention to a tree where *Tirumala hamata* and *Chanapa corinna* were going to roost in extraordinary numbers. *C. corinna* has usually seemed to me to be odourless in both sexes, but on this occasion a captured male appeared to emit a snuffy odour, which was, however, very slight. Mr. Bateson found a spider engaged in devouring a male *T hamata*; both these specimens he gave to me. A male example of *Precis albicincta* Butl. was captured, which had on the underside the whole of the posterior border of the hind-wing, and the greater part of that of the fore-wing, sheared off as if by a straight cut from a moderately sharp instrument.

At midnight the embargo on our voyage was removed, and by 9 a.m. on September 9th we had started. Passing during the day some fine bits of rocky, forest-clad coast, we arrived late at night at Cairns. Next morning (September 10th) a party of us landed and proceeded by train to the Barron Falls and Kuranda, about 22 miles off. The train winds in and out of mountain gorges through splendid tropical scenery. As the track ascends, bananas, pineapples, and oranges are left behind; but the forest trees are green and luxuriant over the whole distance. Rain fell both on the way up and down; but at the Falls and at Kuranda the sun shone brightly, and we saw in the valleys below us great butterflies on the wing, flashing with satiny green; these were *Papilio* (*Ornithoptera*) *priamus euphorion* Gray. The Falls themselves are marvellously beautiful, but we had little time for admiration either here or at Kuranda. For the same reason captures were few, but a certain number of specimens were secured at the latter halting-place. Among these were two males of the dark chestnut-coloured Satyrine *Mydosama terminus* Fabr. Both of these gave an odour of chocolate, noted in one case as "strong," and in the other as "distinct." This observation was confirmed by Prof. H. E. Armstrong, F.R.S., and by Dr. J. W. Scharf, the former of whom thought that the scent of vanilla was also present. The small *Zizera alsulus* Herr.-Sch. ♂ (*Z. lulu* Math.) represented the Lycaenids, and three specimens of *Terias*, belonging to three different sections of the group, were the only Pierines that fell to my net. These were a wet-season female of *T. zoraide* Feld. (noted as having no distinct odour), an intermediate male of *T. hecabe* Linn., which yielded a very slight flowery scent, and an intermediate or wet-season male of *T. lineata* Misk., which likewise had a slight flowery perfume, noticed in the field and confirmed later on board ship. A pretty little Pyralid, *Lygropia quaternalis* Zett. (*amoenalis* Walk.) closes the list.

September 11th found us steaming along close within the Great Barrier Reef, off the northern extremity of the Cape York Peninsula, under a blue sunny sky and over a smooth sea streaked with wonderful shades of blue, green, purple and lilac. The navigation here is said to be very difficult, and our Commander assured us that if we were chased he would undertake to run the pursuing vessel on the reef in a few minutes. Early next morning we were in Torres Strait, and put in for a short time at Thursday Island—one of the most delightful places I have yet seen in the tropics. Bugle calls proceeding from a military camp just above the beach provided a reminiscence of Aldershot, but the wooded hills behind were as different as could be from anything at home. Here, as in Magnetic Island, the ground conditions made collecting difficult; a few specimens were taken and many were missed. Among the former were two males of the fine black and pale green

Papilio aegeus aegeus Don.; both specimens were ragged and yielded no recognisable odour. *Terias herla* McLeay was abundant; a captured male was of the dry-season form. Specimens of *T. lineata* Misk. were dry or intermediate; on scraping the scent-patches of a male, a faint flowery perfume became evident; after a few hours' interval this had ceased to be perceptible. The female was tried for scent, with a negative result; and the same remark applies to *Catophaga ega* Boisd. ♀, which again, as in Magnetic Island, put in an appearance unaccompanied by the male. The absence of scent in these two instances was only in accordance with expectation; but it would not have been surprising to find an odour present in *Danaida affinis* Fabr. ♂; this, however, appeared to be scentless. I failed also, as on previous occasions, to detect any scent, agreeable or otherwise, in *Chanapa corinna* McLeay ♀. Other captures included the only specimen seen of *Neptis consimilis* Boisd., a small Nymphaline marked with two shades of brown—pale and dark; a female *Zizera alsulus* Herr.-Sch., caught and given to me by Professor Armstrong; and two males of *Hypolycaena strabo* Fabr. The latter species was to be seen in some numbers flying about and settling on low bushes which crowned the high slopes overlooking the intensely blue waters of a charming inlet of the sea. Tested for scent, both specimens of *H. strabo* yielded a strong fruity odour, somewhat like that of a very ripe pear; this was confirmed on return to the ship. Dragonflies were numerous everywhere; two males and two females of the dainty *Neurothemis stigmatizans* Fabr. were secured, together with a single specimen of *Orthetrum sabina* Drury, the latter noted as not common. The handsome grasshopper *Gastrimargus pictus* Leach, was plentiful; it is active, and a specimen was captured with some difficulty. *Stropis brunnea* White was also common.

Collecting on Thursday Island, though in most respects delightful, had, besides the roughness of the ground, another slight drawback, viz., the annoying attacks of a large light-green ant, which swarmed in the trees, and was only too ready to drop off on to the passer-by and inflict a sharp and rather painful bite.

Soon after leaving Thursday Island we entertained two visitors in the shape of a pair of pretty little bee-eaters. They flew on board in the afternoon, and roosted at night in the rigging, closely huddled up together. In the morning they had disappeared, having, I hope, found their way back to land. Once more we had to travel at night with few lights, and those covered; the portholes being all shut and blackened on the outside, it may be imagined that the warmth below was considerable. It was known that a German cruiser was not far off. However, we crossed the Gulf of Carpentaria without mishap. The weather continued to be fine and warm as we entered the Arafura Sea. Here we passed through a quantity of yellowish-brown scum, which lay in streaks, and at a little distance imparted a fulvous or almost reddish hue to the surface of the water. This was said to be due to the same organism as that which gives its name to the Red Sea. According to Prof. Seward, F.R.S., it is an Alga, very likely mixed up with diatoms.*

Running past Melville Island on a smooth, pale chalky-green sea, we put in at Port Darwin late in the afternoon of September 15th. Smart ladies and men in white drill came on board to welcome us, and we were forthwith taken in motors to the Botanic Gardens, where we were hospitably received by the Administrator and his wife, and entertained at a delightful open-air tropical tea. Here I had the pleasant experience of meeting with an old pupil, who supplied me with many interesting mementoes of the visit in the shape of shells and crocodile's eggs, together with native implements of war and peace. I was also presented by Mr. Bleeser, a resident, with a few butterflies which had been taken by him in the neighbourhood at various times. These included *Hypocista antirius* Butl., *Atella phalantha* Drury, *Cethosia cyane* Drury ♂, and *Hypolimnas bolina* Linn. ♂.

Next day we were off again, gliding over smooth and almost oily seas on our way to Java. The sun shone in a cloudless sky, and the weather was decidedly warm, though to my mind not unpleasantly so. Sea-snakes were much in evidence, basking at the surface of the calm water.

On September 18th we were passing Timor, and early on the 19th we sighted Lombok. Later in the day we traversed the famous strait between Bali and Lombok, having in sight the two great volcanoes, 10,500 and 12,460 feet high respectively. The Bali mountain was still in view at sunset, and the impression made by the wonderful scenery along "Wallace's Line" is likely to be permanent.

Next morning, as soon as it was light, we found ourselves surrounded by crowds of sampans under sail. These are curiously painted boats with raised and pointed bow and stern, and a very large triangular sail stretched, apex downwards, between two masts, one on each side. A brief visit to the public garden at Sourabaya, our first port of call in Java, resulted in the capture of two males of *Delias periboea* Godt., a species hitherto unrepresented in the Hope collection. Several of these were seen flying high among trees. The two that came within reach of the net had a slight but unmistakable flowery odour, reminding one of wallflower.

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* This Alga (*Trichodesmium* sp.) is a characteristic feature of the tropical oceans at moderate distances from land. In my voyages I have observed it off the coast of Brazil in the region where Charles Darwin described it so graphically in his "Journal of Researches" (pp. 14–15); also in the Red Sea, and especially near the south coast of Ceylon and in the Timor Sea off North-West Australia. Dr. G. B. Longstaff also met with it in the Indian Ocean off Goa (*cf.* "Butterfly Hunting in Many Lands," p. 389). The sailors' name for this plant "sea-sawdust," gives a very good idea of its appearance.—J.J.W.

A fine bit of coast was passed one day, backed by great ranges of jagged mountains. Arriving off Samarang, we came to a stop in a heavy sea about three miles from land. No going ashore was permitted, and the only example of the local fauna secured was the pretty little "yellow underwing," *Hyblaea puera* Cram., which came to light as we lay at anchor.

September 23rd we put in at Batavia, or rather Tanjong Priok, the port. A hurried visit to the world-famed Botanic Garden at Buitenzorg, about 45 miles inland from Batavia, resulted in the capture of a few insects, including *Yphthima philomela* Joh., noted as moderately common; *Precis ida* Cram., and *Neptis leucothoe* Cram., the latter remarkable for its slow, skimming flight near the ground. A beetle, *Galeruca* sp., was taken on the wing. The butterflies seen here were mostly in poor condition.

The speed at which we were obliged to travel prevented any close observation of the country passed through. I retain, however, the impression of an interesting drive through a fertile and highly-cultivated region, thickly populated by a gentle, pleasant-looking, brown-skinned race. The banks of the canal at Batavia were thronged by picturesque groups of women washing clothes, and occasionally themselves, in its limpid if somewhat sluggish waters.

On the way to Singapore, within view of the mysterious heights of Sumatra, we were held up by shots fired across our bows from a big liner armed for war service. She turned out to be the "Empress of Japan," and after boarding us and examining our papers, she allowed us to proceed. At Singapore, reached on September 25th, I was lucky enough to fall in with my sailor son, whose ship had been unexpectedly detained at Hong Kong in consequence of the war. Otherwise he would have missed me, but as it was we were together both at Singapore and Penang.

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(Continued from page 51.)

On September 27th we found an opportunity of visiting the Botanic Gardens, about 3½ miles from the sea front. Here most of the chase was undertaken by my junior, whose bag included the fine swallow-tail *Papilio demolion demolion* Cram. ♂; the Nymphalines *Cupha erymanthis* Drury, *Eulacura osteria* Westw. ♂; *Elymnias nigrescens* Butl. ♂; the Lycaenids *Deudorix domitia* Hew. ♂, *Logania sirwa* Dist. ♂ and ♀, *Nacaduba ? atrata* Horsf. (much worn); and two dragonflies, the brown-winged *Neurothemis fluctuans* Fabr., and *Rhyothemis phyllis* Sulz., a handsome species with black and yellow markings on the hind-wings near the body. Neither *C. erymanthis* ♂ nor *E. osteria* ♂ possessed any recognisable scent; *E. nigrescens* ♂, on the other hand, emitted a strong odour of vanilla. A fragrant flowery smell was also noted in *D. domitia* ♂. My Singapore list likewise includes a fine Uraniid, *Lyssidia docilis* Butl. ♂, which flew on board the s.s. "Montoro," and was brought to me by a Chinese boy in a sadly damaged condition. Here I transhipped to the Japanese liner, "Kashima Maru," and after some considerable delay, possibly due to the exploits of the "Emden," we got under way for Penang. No landing was possible at Malacca, where we stopped at four miles or so from the shore and took in cargo from lighters. The cosmopolitan carrion-beetle *Necrobia rufipes* Fabr. abounded on the ship during this part of the voyage; it readily took flight when disturbed.

Penang, reached on October 3rd, impressed us as a bright and interesting place. My son and I went ashore and took a walk up the Northam and Kelawi Roads, with occasional detours to the sea front. As at Singapore, most of the catching was done by the junior member of the party. The strong vanilla-scent of *Elymnias nigrescens* ♂ was confirmed; three specimens were taken of *Precis atlites* Joh., one in good condition, the others much battered. Lycaenids were represented by three males and a female of *Zizera gaika* Trim.; Satyrids by *Yphthima newboldi* Dist., and *Y. hübneri* Kirby; Danaines by *Radena vulgaris* Butl., and Pierines by three females and a male of *Terias hecabe* Linn. All four of the *T. hecabe* are of the wet season form; the male and one of the females are devoid of markings in the cell of the fore-wing beneath; another female has in that situation two faint markings, and the third female only one. All have the "dog's head" well developed. Other captures at Penang included *Vespa cincta* Fabr., which was common, and two males of the handsome golden-brown *Xylocopa verticalis*, which species was only seen in one place, flying about a hibiscus hedge near the sea. *Necrobia rufipes*, already noted as abounding on board s.s. "Montoro," was common in Penang. This species occurs in Britain, and was also found by Dr. Longstaff at Kimberley in South Africa.

After an adventurous evening excursion by sampan in a heavy sea, with the accompaniments of lightning, thunder and drenching rain, I left Penang on October 4th for Colombo. On October 5th our ship passed within sight of the Nicobar Islands, and after dark on October 7th we made the lights of Ceylon. As on the outward journey, clouds and rain greeted the disembarkation at Colombo, but bright intervals were not infrequent. The first insect to turn up at Colombo was our old friend *Necrobia rufipes*, larger than average specimens from further east, and at night entertainment was provided by a flight of Termites round the hotel lamps, lasting for half-an-hour, more or less. On October 9th I ascended to Kandy by the beautiful railway route, the views along which are world-renowned and deserve their reputation. Kandy itself is delightful in regard of scenery, climate, and surroundings generally. It is true that a thunderstorm began at about 2 p.m. on every day during my stay, and that no day passed without heavy rain. But the mornings, and usually the evenings were fine, and the air was always fresh and exhilarating. My quarters on the shore of the charming lake, within sight (and hearing) of the famous Temple of the Tooth, could hardly have been bettered for interest and comfort. The eulogy passed by Dr. Longstaff on Lady Horton's Drive ("Butterfly Hunting in many Lands," Longmans, 1912: p. 109) accords with my own experience, and is, I think, no whit too favourable. Along this pleasant road, cut through the jungle that clothes the hillside, butterflies were numerous so long as the sun shone. Many, however, scarcely deigned to come within reach of the net. From time to time the splendid black and gold *Papilio* (*Ornithoptera*) *darsius* Gray, would be seen; generally too high up for capture. Now and then it descended, and on one occasion I actually had a fine male in my net; but eventually it escaped and I did not get another chance. More often in view was *P. pammon* Linn. Dr. Longstaff states that in the only specimen of this *Papilio* in which he detected any odour, it was somewhat agreeable; a male, however, tested by me on October 11th is noted as "smelling like a kitchen sink." Pierines were very little in evidence; the only ones taken belonged to the *hecabe* group of *Terias*, and were all of the wet season phase. Two males of *T. silhetana* Wallace, were observed playing together; one of these had a slight flowery scent, the other appeared to be odourless, as also did a male and female of *T. rotundalis* Moore (? *T. sari* Horsf.)*.

The common Danaine in Lady Horton's Drive, as elsewhere about Kandy, was *Parantica aglea* Cram. It was noted by me as flying slowly, being easily caught, and possessing very great tenacity of life. One specimen had a slight smell suggestive of old upholstery; in another a scent, not particularised, was doubtfully present; in three others, including one taken in Colombo, no odour was detected. These five specimens were, curiously enough, all females. A male of *Crastia asela* Moore, taken in the path above the old cemetery at Kandy, was similarly noted as tenacious of life, and as having no perceptible odour. Dr. Longstaff (*loc. cit.*, pp. 496, 7) says, "I am satisfied that in *P. aglea* the scent is more transitory, possibly more volatile, than in the majority of scent-yielding butterflies . . . . As with *Parantica* the scent of *Crastia* would appear to be more volatile than in the *Pierinae* or in *Danaida*." This accords with my own observations. Among Nymphalines, *Neptis varmona* Moore, was common; like other species of the genus it has a slow, sailing flight. Two specimens, ♂ and ♀, were noted as scentless; in a third, however, apparently a female, a faint flowery scent seemed to be present. A male taken at *Lantana* flowers close to the lake had no distinct odour. It is interesting in connection with these observations that Dr. Longstaff writes as follows (*loc. cit.*, p. 502), "*Neptis jumba* Moore (Ceylon, 1908). A faint sweet chocolate scent was detected in a male in the house. A somewhat similar scent was suspected in another male and in a female. On the other hand, no scent was recognised in the much commoner *N. varmona* Moore." One of the most remarkable frequenters of Lady Horton's Drive was *Cethosia nietneri* Feld.; an ammoniacal scent was noted in a captured female. With regard to *Cynthia asela* Moore, I agree with Dr. Longstaff (*loc. cit.*, pp. 112, 348) that it "seems to like sailing about over the trees"; also that it is hard to get in good condition. He finds in the male a faint scent which he compares to "sassafras and to French polish." The only specimen tested by me (a ♂) appeared to have a scent, the nature of which I failed to determine. No odour was detected in a ragged *Cirrochroa cognata* Moore, ♂; but a slight fusty smell was somewhat doubtfully recognised in *Ergolis ariadne* Linn., ♀. This specimen had a large piece cut cleanly out of the right fore-wing. A specimen of *Vanessa haronica* Moore (the "Blue Admiral") behaved much like an English *Vanessa*. It settled in the road with wings expanded, closing and opening them again from time to time, and when disturbed returned persistently to the same place. On its intermittent flights it was joined by another one, which eluded capture. No scent was found in the specimen taken. The commonest Satyrines in Lady Horton's Drive were *Nissanga patnia* Moore, and *Yphthima ceylonica* Hew. A somewhat worn male of the former species was odourless, as were also two females; but a fresh male specimen emitted a strong fragrant scent, which I compared to that of caramel with a touch of chocolate. Dr. Longstaff (*loc. cit.*, p. 346) says of *N. patnia*, "twice I suspected that it had a scent, though it cannot have been strong." It evidently varies in individuals. The same is probably true of *Y. ceylonica*, since in two males I found a strong smell of chocolate, in one case confirmed in the house; and of a third male I note "odour (in field) slight or absent. No odour detected in the house." Three females were likewise scentless. Dr. Longstaff reports (*loc. cit.*, p. 346) that "the males appeared to have a very slight scent suggestive of chocolate."

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* For an interesting discussion of certain forms of the *hecabe* group, see Dr. Longstaff's "Butterfly Hunting in Many Lands," Longmans, 1912, pp. 353, 354.

Another Satyrine taken in Lady Horton's Drive was *Orsotriaena mandata* Moore. This was only seen in one place—just above the paddy fields near the end of the Drive. Dr. Longstaff (*ibid.*) also found it to be very local, and only common in one place—along the edge of a paddy field. Before leaving Kandy, however, I found it in another locality. This was Wace Park, on the wooded slopes overlooking the lake; here two males were playing together in the rain. One was examined for scent without result; the other at first appeared to be odourless, but on spreading out the tuft of hair-scales on the left side, I at once became sensible of an odour which I cannot otherwise describe than by calling it pleasantly aromatic. Close to the aforesaid paddy-fields, I made practical acquaintance with the land-leech of Ceylon—a noisome and insinuating beast.

Perhaps the commonest Lycaenid in Lady Horton's Drive was *Loxura arcuata* Moore. Several were seen, darting rapidly about and settling from time to time on the upper side of leaves. It is a particularly wary insect. No scent was found in *L. arcuata*; *Nacaduba atrata* Horsf., ♂, on the other hand, which was captured while flying about a patch of old bullock-dung in the road, had a distinct flowery smell, still perceptible on the following day.

A female caught at the same time and place was odourless. A sweet flowery scent was noticed in two males of the same species by Dr. Longstaff (*loc. cit.*, p. 505). One of the most striking denizens of the Drive, also encountered on the opposite side of the lake, was *Talicada nyseus*, an interesting Lycaenid with curiously variegated underside. Other captures included *Chalcosia thallo* Linn., a pretty moth, white with touches of bronzy green, and *Macaria nota* Walker, a Geometrid with a somewhat butterfly-like aspect. *C. thallo* was found by Dr. Longstaff (*loc. cit.*, p. 360), to have "a peculiar, disagreeable, musty odour, not at all strong and seemingly present in both sexes." The only specimen examined by me appeared to be scentless. At one place winged Termites were swarming (October 11th); one of these shed two wings in the cyanide bottle; another reached home intact. The blue-banded bee, *Podalirius zonatus* Linn., ♀, ends the list of captures in Lady Horton's Drive.

A visit to the famous Botanical Gardens at Peradeniya was not productive of insect booty. The day was dull, and from time to time the rain fell in torrents. The usual afternoon thunderstorm did not improve matters, and much of my time was spent under the roof of a hut on the slope overlooking the river. Between the showers, *Yphthima ceylonica* was to be seen in plenty. Immediately after rain, or even before the last drops had fallen, numbers of this cheerful little Satyrid appeared on the wing; flying near the ground, and settling with wings sometimes open, sometimes closed.

At a cluster of *Lantana* flowers, on the east shore of the lake, I took *Precis iphita* Cram. This butterfly was on one occasion noted by Dr. Longstaff at flowers, though he observes that this is not a common habit of the species (*loc. cit.*, p. 64). My specimen, a male, possessed no distinct odour. *Neptis varmona* was taken at *Lantana* flowers in the same place, which also yielded *Talicada nyseus*, *Yphthima ceylonica*, and a handsome Hemipteron, *Ectrychotes* sp., captured on the wing. A pale-coloured Arctiid moth, *Migoplastis alba* Moore, ♀, picked up in the road at Kandy by a fellow-traveller, Mr. C. Skyrme; and a metallic-green beetle, *Euchlora* (*Anomala*) *dussumieri* Blanch., found by the same gentleman in the road between Kandy and Peradeniya, complete the tale of my collecting at Kandy.

On returning to Colombo, I revisited my old locality; war conditions, however, proved to be adverse to collecting. The best spot was in occupation by the military; after capturing a single *Parantica aglea* I was challenged by an armed sentry, and finding him impervious to reason, I thought it best to withdraw. Other places were unproductive, but in the Park I saw *Delias eucharis* Drury, on a flower—the only specimen of this common butterfly that has crossed my path.

The remainder of the voyage was entomologically uneventful. On the morning of Oct. 16th, a fine view was had of Cape Comorin; and on Oct. 20th, R.M.S. "Otway" was in the Gulf of Aden. Here a pretty Sphingid came on board—small, and with a stripe of old gold on each side of its body. It was boxed, but eventually made good its escape. A *Macroglossa* (?) was seen flying about the ship off Suez. At Port Said a fine specimen of *Mantis religiosa* was secured on deck. On Nov. 2nd we were once more at Gibraltar. The day was perfect—fine, warm, and sunny. Many butterflies were on the wing—whites and Vanessas. Hibiscus, plumbago, and other flowering shrubs were well out in bloom. The "pepper trees" (*Schinus molle*) were bright with red berries. Altogether, Gibraltar in November presented a decidedly attractive appearance. But our stay here was short, and after experiencing some rough weather off Cape St. Vincent, we made Plymouth safely on the morning of November 6th.

Wadham College, Oxford:

November 24th, 1915.

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SOME *LEPIDOPTERA* FROM EASTERN FRANCE.

BY F. C. WOODFORDE, B.A., F.E.S.

The following account of some *Lepidoptera* captured in the extreme north of the Department of Haute Saône from July 21st to September 25th, 1920, may be interesting to some of your readers. During the last week of July, *Papilio machaon* and *Colias hyale* were common in the permanent clover fields, and both when bent on feeding were easy to catch, but many flew wildly about without taking any notice of the flowers, and were then quite impossible. During that week and the next *Lycaena baton* and *semiargus* were also common in the clover-fields, and *Chrysophanus dorilis* was not uncommon. On rough ground, on the outside of a very large wood, *Lycaena arion* showed itself, but only in very small numbers, and I did not see a dozen altogether. Of *L. argiades* I caught two specimens, one on July 25th, the other on September 11th. *L. argiolus, L. coridon,* and *L. aegon* were all very scarce, and of *C. phlaeas* I did not see a single specimen during the whole of my stay. At the end of August I saw and caught two worn specimens of *Zephyrus betulae*, male and female. This is a butterfly that seldom is seen on the wing, but from the quantity of sloe growing everywhere in the district, I suspect that plenty of larvae could be taken in June.

C. edusa was flying from July 25th up to the beginning of September, but was quite uncommon, and I did not see more than a dozen specimens altogether.

During August, *Aglais urticae, Vanessa io, Pyrameis cardui* and *atalanta* were flying, but none of the species were in abundance. One very worn *Polygonia c-album* was caught at the end of July, and a freshly-emerged specimen was seen about the middle of September. *Limentis sibylla, Dryas paphia,* and *Argynnis adippe* were common, but very much worn up to the middle of August. One specimen, very worn, of *A. aglaia* was seen at the end of July. From August 7th to 29th *Brenthis dia* was in evidence, but not at all common. Two or three specimens were quite fresh. On August 12th I took a single example of *B. selene* in very good condition, but saw no others. A worn specimen of *Melitaea athalia* was taken on August 28th; of the Satyrines, *Epinephele jurtina, E. tithonus,* and *Coenonympha pamphilus* all through August were literally swarming. In the first half of that month *Erebia aethiops* were flying on the rough ground mentioned above, and one or two were seen in the middle of the wood in an open space. *Pararge aegeria* var. *egerides* showed itself, but was decidedly rare. Early in the month some very worn specimens of *Melanargia galatea* were still flying.

In September, *Pararge megaera* and *P. maera* were not uncommon, all the latter being of the *adrasta* form. *Pieris brassicae* and *rapae* were common, especially the latter, but *P. napi* was not at all so. *Leucophasia sinapis* flew in the fields and in the sides of the wood, but was by no means common. *Gonepteryx rhamni* was numerous at the end of August, but after the first week of September, which was wet and cold, very few were to be seen; even on bright sunny days the cold weather apparently drove them to hibernation. I have not yet mentioned one butterfly which swarmed in almost incredible numbers all through August, *Lycaena icarus*. On several occasions I saw over one hundred sitting close together on damp spaces, sometimes in a space of less than two square yards, all males. Only once did I see a female in these assemblies. Although I examined them very carefully, I could see no signs of a variety among them. As I have said, the first week of September was cold and wet; and this seemed to have a remarkable effect on the Vanessids, for all through that month I did not see a single specimen of *A. urticae*, *V. io*, or *P. cardui*, less than a dozen *P. atalanta*, and only one *P. c-album*, yet after the first week the days were bright and sunny, though the nights were decidedly cold.

I did no night work during my visit for various reasons, one being that it was impossible to get materials for sugaring, another that I am not now so young or energetic as I once was, so that not very many moths came in my way. A few, however, came into the room to the light through the window, among them a beautifully fresh specimen of *Hadena atriplicis* and another of *Leucania albipuncta*, one *A. pyramidea*, and, of course, many *Neuronia popularis*. In the daytime a single specimen of *Macroglossa stellatarum* in fresh condition was taken, and a few minutes afterwards a very worn-out specimen of *Hemaris tityus* flying about a scabious flower. In the clover-fields, *Euclidia glyphica* and *Strenia clathrata* were common, as was, later on, *Anaitis plagiata*. A few *Acontia luctuosa*, *Acidalia ornata*, and *A. rubiginata* also were seen, as were odd specimens of *Camptogramma bilineata*, *Fidonia atomaria*, and *Cidaria prunata*.

I was much struck by the fact that so few species occurred that are not taken in the British Isles. With regard to that important point in field entomology—the weather—I left cold, dull, and unpleasant conditions in England on July 21st to find splendidly bright hot weather in France, which, except for occasional thunderstorms, lasted up to the very end of August.

Oxford.
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